

CALIFORNIA ASTER YELLOWS ON VEGETABLE  
AND SEED CROPS<sup>1</sup>HENRY H. P. SEVERIN<sup>2</sup> AND NORMAN W. FRAZIER<sup>3</sup>

## INTRODUCTION

THE INVESTIGATIONS of host plants of aster yellows are covered by three reports. The present paper is confined to the work with aster yellows on vegetable and seed crops. One other paper in this issue describes the disease on ornamental flowering plants (Severin and Freitag, 1945). Weeds experimentally and naturally infected are discussed in a third paper (Frazier and Severin, 1945).

In 1902<sup>4</sup> Smith described aster yellows, especially as it affects the flower; he was the first to notice it in California. The disease is now generally distributed in most counties of the state. Among economic plants, celery is seriously affected (Severin, 1929a) in certain years. During 1931 a general outbreak occurred in the Sacramento Valley, and celery in many fields was plowed under. Lettuce, carrots, parsley, parsnip, and potato (Severin, 1929a, 1932, 1940) have been demonstrated to be naturally infected; but the disease is of no economic importance at present.

Field investigations of other host plants of this virus were conducted from 1925 to 1943. Several new vegetable host plants were noted, as recorded in this paper. The infection of seed crops received special attention, and surveys were made of seed farms and the ranches of seed companies. Attempts were made to recover the virus from naturally infected host plants. The symptoms were studied.

## METHODS

The method of recovering the virus from naturally infected host plants and the production of noninfective leafhoppers were the same as in previous investigations (Severin 1929a, 1942). A detailed account of methods is given in the third paper of this series (Frazier and Severin, 1945).

<sup>1</sup> Received for publication April 28, 1944.

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<sup>4</sup> See "Literature Cited" at the end of this paper for complete data on citations, referred to in the text by author and date of publication.

## HOST RANGE OF VIRUS

The host range of the aster-yellows virus among economic plants naturally infected includes 11 vegetables, 12 seed crops belonging to 14 species in 12 genera in 6 families, including those previously reported (Severin, 1929a, 1932, 1940). The season's duration of each plant is given in the following list:

## Chenopodiaceae:

*Spinacia oleracea* L.,\* spinach, unknown variety; seed crop; annual

## Compositae:

*Cichorium Intybus* L., chicory; seed crop; perennial

*Cichorium Endivia* L., endive; vegetable; annual or biennial

*Scorzonera hispanica* L., black salsify; vegetable; perennial

*Lactuca sativa* L.\* lettuce; vegetable (Severin, 1929a) and seed crop; annual

*Lactuca sativa* L. var. *longifolia* Lam., Romaine lettuce; vegetable; annual

## Cruciferae:

*Brassica oleracea* L. var. *capitata* L., cabbage; vegetable and seed crop; biennial

*Brassica oleracea* L. var. *botrytis* L., cauliflower; seed crop; biennial

*Brassica oleracea* L. var. *italica* Plenck., sprouting broccoli; seed crop; biennial

*Raphanus sativus* L., Long White Chinese radish; vegetable and seed crop; annual or biennial

## Liliaceae:

*Allium Cepa* L., onion; vegetable and seed crop; biennial

## Solanaceae:

*Solanum tuberosum* L., potato (Severin, 1940); herb

## Umbelliferae:

*Daucus Carota* L. var. *sativa* DC., Short White and Yellow Belgian carrots; vegetable (Severin, 1932) and seed crop; annual or biennial

*Petroselinum crispum* Nym., Double Curled parsley and unknown variety; seed crop; biennial or perennial

*Petroselinum hortense* Hoffm. var. *radicosum* Bailey, Hamburg or turnip-rooted parsley; vegetable (Severin, 1932); biennial

*Apium graveolens* L. var. *dulce* DC., Golden Self-Blanching celery; vegetable (Severin, 1929a) and seed crop; Utah celery, vegetable; biennial or perennial

*Apium graveolens* var. *rapaceum*, celeriac; vegetable; biennial

*Pastinaca sativa* L.,\* Hollow Crown parsnip; vegetable (Severin, 1932) and seed crop; biennial

The virus overwinters in biennials and perennials; it also is carried over by overwintering leafhoppers.

The virus was recovered by previously noninfective short-winged and long-winged aster leafhoppers from the naturally infected host plants and transferred to healthy aster or celery.

## LILIACEAE, LILY FAMILY

Onion (*Allium Cepa*) plants grown from bulbs were collected on September 22, 1941, in a canyon of the Montara Mountains. These specimens showed chlorosis of the leaves, which on some plants drooped and on others were twisted and intertwined. Onions grown for seed production near Cotati were

\* The asterisk indicates overlapping host ranges of California and New York aster-yellows viruses.

also shown to be naturally infected with aster yellows during the summer of 1943. Since the symptoms were not those of yellow dwarf (Drake, Tate, and Harris, 1932, 1933), tests were made to recover the California aster-yellows virus from the diseased onions. Attempts were made to infect healthy onion plants experimentally by means of different species of leafhoppers.

The virus was recovered from naturally infected onion by previously non-infective short-winged aster leafhopper, *Macrostelus divisus* (Uhl.), and by the long-winged race of the same species. The former transmitted it to healthy celery. The long-winged aster leafhopper on celery usually dies before the so-called virus incubation period is completed in the insect; hence it was transferred to healthy asters and transmitted the virus to them.

TABLE 1  
LONGEVITY OF FIVE LEAFHOPPER VECTORS ON ONION PLANTS

Common and scientific names of leafhoppers	Lots of 20 adults used	Longevity of males		Longevity of females	
		Range	Average	Range	Average
	<i>number</i>	<i>days</i>	<i>days</i>	<i>days</i>	<i>days</i>
Short-winged aster leafhopper, <i>Macrostelus divisus</i> (Uhl.).....	24	3-10	6.7	13-21	18.4
Long-winged aster leafhopper, <i>Macrostelus divisus</i> (Uhl.).....	17	4-8	5.6	8-22	13.6
Mountain leafhopper, <i>Colladonus montanus</i> (V. D.).....	9	3-6	4.5	5-10	7.5
Geminate leafhopper, <i>Idiodonus geminatus</i> (V. D.).....	9	4-12	7.0	4-10	6.2
Acute-winged leafhopper, <i>Acinopterus angulatus</i> Law.....	4	31-33	32.0	18-26	22.0

Danvers Yellow Globe, Red Wethersfield, and Sweet Bermuda onion plants grown from sets, and Danvers Yellow Globe grown from seeds were all experimentally infected. These onion plants were exposed to lots of either 20 infective short-winged or 20 long-winged aster leafhoppers until the insects died on the plants. After symptoms appeared on the infected onion plants, the virus was recovered by lots of 20 previously noninfective short-winged or long-winged aster leafhoppers and transferred to healthy celery and asters respectively.

The long-winged aster leafhopper, which was the most efficient vector of the virus to onion, was abundant in the canyons of the Montara Mountains. Short-winged aster leafhoppers were captured on weeds growing in onion fields and along roadsides near Cotati.

The virus was also transmitted to onion plants by the mountain leafhopper, *Colladonus montanus* (V. D.) = (*Thamnotettix montanus* V. D.); the geminate leafhopper, *Idiodonus geminatus* (V. D.) = (*Thamnotettix geminatus* V. D.); and the acute-winged leafhopper, *Acinopterus angulatus* Law.

Table 1 shows the longevity of the last living male and female in lots of 20 adults of the 5 vectors on onions. The 5 vectors failed to complete the nymphal stages on onions.

The first symptom on experimentally infected onion plants grown from seeds or sets is a yellowing of the basal portion of the youngest leaves, gradually spreading until these entire leaves are affected. Sometimes the chlorotic

leaves twist and intertwine as described on celery, carrot, Hamburg or turnip-rooted parsley, and parsnip (Severin 1929a, 1932). Sometimes, in the later stages of the disease, the leaves droop and wilt, and the plants die.

The symptoms on naturally infected onions grown for seed vary in different plants. Onion plants infected before the peduncle developed often showed twisted and intertwined leaves, yellow or orange in color. Frequently the pedicels, or flower stems, in the terminal umbel were greatly elongated (plate 1, A). The most striking symptom was the production of bulbils or bulblets (Bailey, 1924) instead of seeds in the umbel (plate 1, B). The bulblets developed yellow or green leaves (plate 1, C). Often each bulblet was on a pedicel (plate 1, D), or some were sessile and others on pedicels (plate 1, E). Experimentally infected seed crops grown from sets also developed these symptoms. The manifestations of aster yellows on the umbels are called "onion shaggy head" or, according to KenKnight (1943), "frizzle top."

As a result of scheduling the reading of a paper by the senior author, however, requests for information were received from W. J. Virgin<sup>6</sup> and Glen KenKnight.<sup>7</sup> In response, California aster yellows on onions was described to them and identified in Virgin's photographs of diseased onions. The evidence for natural and experimental infection of this vegetable was reported to them, and the vectors were given. Though no mention was made of the source, it was presumably on the basis of this correspondence that KenKnight (1943), apparently failing to realize that the information was given confidentially in advance of publication, issued the following statements:

There are two strains of the aster-yellows virus, the Eastern or Typical Strain and the Western or California Strain. These differ in host range. It is possible that both are present in Idaho. Both strains of the virus are spread by the six-spotted leafhopper, and it has been shown that the California Strain can be spread by about twenty species of other leafhoppers.

Onion plants affected with aster yellows ("frizzle top") produce seed stalks which have leafy structures instead of floral parts. A healthy and diseased seed head are shown on the cover of this leaflet.

Bulblets separated from the umbels from infected plants were planted, and some grew. Previously noninfective short-winged and long-winged aster leafhoppers recovered the virus from these onions and transferred it to healthy celery and asters respectively.

The incubation period of the disease in onion plants grown from sets ranged from 9 to 23 days, an average of 16.3 days; and in Danvers Yellow Globe seedlings from 10 to 20 days, an average of 15.0 days, when the basal portion of the youngest leaves became chlorotic.

Kunkel (1926, 1931) reported that he experimentally transmitted the New York aster-yellows virus by means of the aster leafhopper, *Macrosteles divinus* = (*Cicadula sexnotata* Uhl.), to 184 species of plants in 151 genera belonging to 38 families. But he does not list a single plant of the family Liliaceae, to which the onion belongs. All our attempts to transmit the eastern

<sup>6</sup> Virgin, W. J. Associate Plant Pathologist in the Idaho Agricultural Experiment Station; letter to senior author dated July 15, 1942.

<sup>7</sup> KenKnight, Glen. Associate Plant Pathologist in the Idaho Agricultural Experiment Station; letter to senior author dated January 15, 1943.

aster-yellows virus<sup>8</sup> to onions by means of short-winged and long-winged aster leafhoppers were failures.

Doolittle and Wellman (1934) reported that southern celery-mosaic virus, transmitted by the cotton or melon aphid, *Aphis gossypii* Glover, was the



Fig. 1.—Celeriac naturally infected with aster yellows, showing shortened, curved, and twisted petioles of youngest leaves.

first definitely established case of a mosaic virus affecting both dicotyledonous and monocotyledonous plants. The natural infection of onions with California aster yellows is the first example of a leafhopper-transmitted virus of the yellows group affecting both dicotyledonous and monocotyledonous plants.

<sup>8</sup> Infected asters were received from L. M. Black, Rockefeller Institute for Medical Research, Princeton, New Jersey.

## UMBELLIFERAE, PARSLEY FAMILY

Celery (*Apium graveolens* var. *dulce*) grown for seed was demonstrated to be naturally infected with aster yellows. Diseased plants were common in the fields between Davis and Sacramento during the outbreak in 1931. The in-



Fig. 2.—Parsley plant, grown for seed, naturally infected with aster yellows, showing numerous axillary shoots at the apical end of the main seed-stalk. Umbels failed to develop.

fecting plants were stunted and chlorotic, with numerous bunched shoots at the apical ends of the branches (plate 2, C). Severin (1929a) has described the symptoms on celery in a previous paper.

Celeriac (*Apium graveolens* var. *rapaceum*) was proved to be naturally infected with aster yellows. Diseased plants were common in a commercial vegetable field near San Leandro during the autumn of 1936. The petioles of

the innermost or youngest leaves are shortened, curved, and twisted (fig. 1); sometimes they intertwine.

Parsley (*Petroselinum crispum*) grown for seed was shown to be naturally infected with aster yellows. In 1933, 1 per cent of Double Curled parsley plants had been infected with the virus before transplantation in the San



Fig. 3.—Parsley plants, grown for seed, naturally infected with aster yellows, showing dwarfed compound umbels.

Juan Valley. Diseased plants after transplantation in the field are chlorotic and stunted, with a dense growth of adventitious shoots (plate 2, *E*). The petioles of some of the leaves are twisted (plate 2, *D*). A previous paper (Severin, 1932) describes the symptoms on three varieties of parsley experimentally infected, together with the incubation period of the disease.

Parsley, grown for seed, with dense clusters of axillary shoots on all stems and with deep green leaves was common on seed farms in the Salinas Valley. The axillary shoots form a compact cluster of leaves at the apical ends of the main and lateral seedstalks (fig. 2). The lateral seedstalks are short and

bear upright secondary shoots. Umbels fail to develop on such plants (fig. 2). The virus was recovered from plants showing these symptoms and was transferred to healthy asters and celery.

On the same seed farm there were occasional infected parsley plants that did develop umbels. The pinnately compound leaves on these plants are chlorotic and curled outward, and the compound leaves are dwarfed or absent on the lateral seedstalks (fig. 3). The flowers of the compound umbels are green instead of yellowish green. The petals and stamens are replaced by green leafy structures.

Carrots (*Daucus Carota* var. *sativa*) infected with aster yellows before transplanting develop a dense cluster of dwarfed, chlorotic, upright adventitious shoots (plate 3, A, B) with dwarfed umbellets (plate 3, B). Carrot plants, grown for seed, infected with aster yellows after transplantation are conspicuous in the field during the blossoming period; the flowers are yellowish green, in contrast to the showy white flowers on healthy plants. The outer raylets in the umbellets and the pedicels are longer than normal (plate 3, C). The calyx tube is longer than in healthy flowers. The peduncles are chlorotic. On some infected plants the leaves are purple; on others the margins of the pinnate decompound leaves are purple, and the remainder is green (plate 8, B). The leaves on some plants, probably in the advanced stage of the disease, are yellow, except that the midrib and lateral veins are green (plate 8, A). There is an increase in the number of rootlets on infected carrots (plate 3, D), a condition which, in the sugar beet infected with curly top (Severin, 1929b), has been described as "hairy" or "woolly root" or "whiskered beets."

The symptoms, the recovery of the virus from naturally and experimentally infected carrots, and the incubation period of the disease in 3 white, 1 yellow, and 7 orange varieties have been described in a previous paper (Severin, 1932).

Parsnip (*Pastinaca sativa*), grown for seed, naturally infected with aster yellows is chlorotic, both leaves and stems. The stems are sometimes curled (plate 4, A), and the peduncles twisted. The compound umbels on diseased plants are yellow; on healthy plants greenish yellow. The raylets and pedicels on infected plants are elongated (plate 4, B). Sometimes numerous compound umbels develop, forming a cluster of tangled raylets and pedicels (plate 4, C).

#### CRUCIFERAE, MUSTARD FAMILY

Cabbage (*Brassica oleracea* var. *capitata*) near Irvington in 1939 was found to be naturally infected with aster yellows. Such plants are dwarfed and usually form no heads or very small heads. The youngest leaves exhibit a clearing of the veins. As the leaves grow older, the veins swell on both upper and lower surfaces, and become white. The youngest leaves are a normal green, the older leaves chlorotic, and the oldest leaves white. Successive older leaves become more and more outwardly and downwardly curled toward the petioles.

Cauliflower (*Brassica oleracea* var. *botrytis*) grown for seed near Irvington and in the Salinas Valley was naturally infected. Often the lateral flower stalks are curved or twisted (plate 5). The flower clusters are usually dwarfed

on most of the stalks, with short peduncles and pedicels. Toward the apical end of the stems, however, the peduncles and pedicels are often elongated, forming a tangled cluster. No study has been made of the flower abnormalities of cauliflower naturally infected with aster yellows, since the flower buds were not expanded.

Sprouting broccoli (*Brassica oleracea* var. *italica*) near Irvington in 1939 showed symptoms of aster yellows. A profuse proliferation of the inflorescence occurs, accompanied by phyllody, the tendency of the floral organs to resemble leafy structures (plate 6, A); and by virescence, or greening, of the flowers. The pedicels or stems of the flowers are elongated. The sepals are



Fig. 4.—Radish plants, grown for seed, naturally infected with aster yellows, showing proliferation of the flowers; the petals, stamens, and gynoecium are replaced by leafy structures.

enlarged, the petals reduced; both are leafy and green. The stamens are usually reduced, but often enlarged and green; when enlarged the pollen sacs expand to form leafy structures; the filaments are elongated into a stem; and thus the stamens are replaced by bipinnate leafy structures (plate 6, B). The gynoecium is elongated, sometimes club-shaped; the carpels bifurcate and leafy (plate 6, B).

Radish (*Raphanus sativus*), grown for seed, manifesting natural infection with aster yellows was common on seed farms in the Salinas Valley. Tufts of green flowers occur on the apical ends of the seedstalks instead of the showy white flowers seen on healthy plants of the same variety. A proliferation of the flowers occurs, successive flowers with long pedicels developing from the ovaries (fig. 4). Often the petals, stamens, and gynoecium are replaced by leafy structures (fig. 4).

Long White Chinese radish collected near Irvington was demonstrated to be naturally infected with aster yellows.



Fig. 5.—Longitudinal sections of Romaine lettuce: *A*, flattened head of diseased plant showing outward-curved, dwarfed, chlorotic youngest leaves; *B*, upright and narrow or columnar head of healthy plant.

## COMPOSITAE, COMPOSITE FAMILY

Lettuce (*Lactuca sativa*) grown for seed in the Santa Clara Valley was a failure in 1943, owing to aster yellows and spotted wilt. Infected plants often fail to develop flower stalks. Some plants develop a short flower stalk; on them the lower leaves are normal, whereas the youngest leaves are yellow, dwarfed, and curled outward instead of inward. The stems are dwarfed, and often the veins and veinlets are cleared. The most conspicuous symptom on plants with long flower stalks is the upright or vertical branches, with sec-

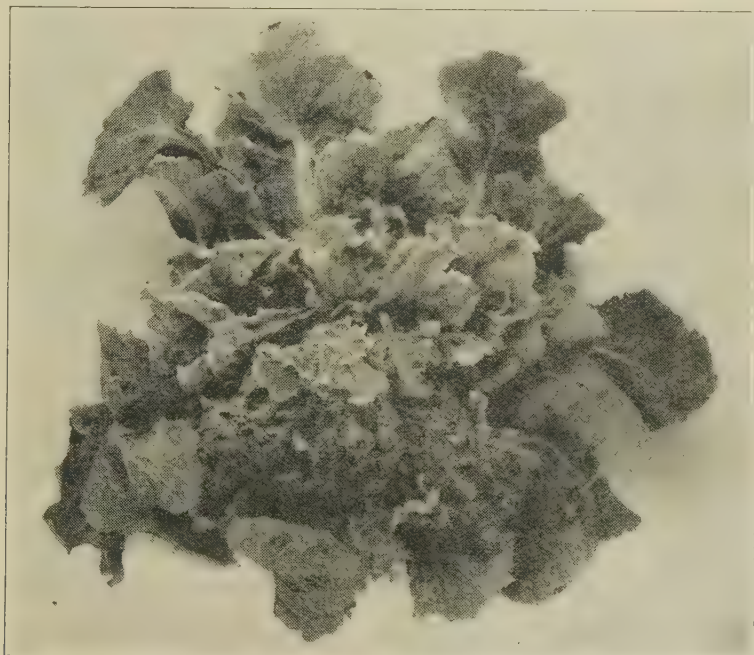


Fig. 6.—Endive naturally infected with aster yellows, showing stunted, flattened, and yellow leaves, with heart leaves curled outward and dwarfed.

ondary shoots arising from the axil of the leaves at the apical end of the erect flower head (plate 7, A). Sometimes the branches are curved or twisted (plate 7, B). A reliable symptom in late-infected plants is the enlarged flower buds (plate 7, C); the rays are green instead of yellow.

Romaine lettuce (*Lactuca sativa* var. *longifolia*) in the South San Francisco vegetable gardens was proved to be naturally infected with aster yellows. The head is flattened in infected plants (fig. 5, A), instead of upright and narrow or columnar as in healthy plants (fig. 5, B). A longitudinal section of the head of a diseased plant shows outward-curved, dwarfed, chlorotic leaves (fig. 5, A).

A single chicory (*Cichorium Intybus*) plant 6 feet tall, grown for seed on a farm in the Santa Clara Valley, was naturally infected with aster yellows. The most striking symptoms are the numerous axillary shoots on all branches,

The basal part of these shoots and the midrib of the leaves are white. The margin of some of the leaves is undulating or wavy; sometimes the leaf is twisted into a corkscrew (plate 8, *C*). The flowers, in heads, are bright azure blue on healthy plants; but on the infected plant the buds are dwarfed, fail to expand, and are surrounded by linear leafy structures (plate 8, *C*).

Endive (*Cichorium Endivia*) in the South San Francisco and Colma vegetable districts was naturally infected with aster yellows.<sup>9</sup> The symptoms on



Fig. 7.—Spinach plant, grown for seed, naturally infected with aster yellows, showing chlorotic, dwarfed seedstalks.

endive are somewhat similar to those on lettuce. The most striking symptoms are stunting of the entire plant and yellowing of the leaves (fig. 6).

Black salsify (*Scorzonera hispanica*) in the Colma vegetable districts was also naturally infected. The long-winged petioles intertwine. The youngest leaves are chlorotic; but the older leaves are green.

#### CHENOPODIACEAE, GOOSEFOOT OR SALTBUSH FAMILY

Spinach (*Spinacia oleracea*) grown for seed was rarely found to be naturally infected with aster yellows. Infected plants are chlorotic and dwarfed, with short seedstalks (fig. 7). The youngest leaves show a clearing of the veins and veinlets.

<sup>9</sup> We are indebted to C. M. Tompkins, who collected endive and black salsify that was naturally infected with the aster-yellows virus.

## HOST-RANGE DIFFERENCES OF CALIFORNIA AND NEW YORK ASTER YELLOWS

Kunkel (1926, 1931), in his host-range studies, lists no plant of the family Liliaceae. All our attempts to infect onions with the virus of New York aster yellows were unsuccessful.

Kunkel (1926, 1931) lists eight vegetables as host plants of the New York aster-yellows virus. Three of these, indicated by an asterisk in the list on page 574, are also hosts of the California aster-yellows virus.

### SUMMARY

The host range of aster yellows among economic plants naturally infected includes 11 vegetables and 12 seed crops. These belong to 14 species in 12 genera in 6 families, including those previously reported (Severin, 1929a, 1932, 1940). The virus overwinters in biennials, perennials, and overwintering leafhoppers.

The symptoms are described for each species or variety proved to be naturally infected.

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## PLATES





Plate 1.—Onion naturally infected with aster-yellows virus: *A*, pedicels in terminal umbels, greatly elongated; *B*, sessile bulblets developed in the umbel instead of seeds; *C*, sessile onion bulblets that have developed yellow or green leaves; *D*, onion bulblets and flowers on pedicels; *E*, sessile onion bulblets and flowers on pedicels in same umbel.



Plate 2.—*A, B*, Shoot and umbel from a healthy celery plant; *C*, cluster of shoots at the apical end of a branch from a celery plant, grown for seed, naturally infected with aster yellows; *D*, twisted petioles from parsley plants, grown for seed, naturally infected with aster yellows; *E*, parsley plants showing dense growth of adventitious shoots.



Plate 3.—Carrot plants, grown for seed, naturally infected with aster yellows; A, dense cluster of dwarfed, upright, adventitious shoots; B, numerous axillary shoots with dwarfed umbellets; C, umbellets showing elongated raylets and pedicels; D, carrot showing increase in number of rootlets.



Plate 4.—Parsnip plants, grown for seed, naturally infected with aster yellows; *A*, curled and twisted stems; *B*, elongated raylets and pedicels; *C*, compound umbellets showing clusters of tangled raylets and pedicels.



Plate 5.—Cauliflower plant, grown for seed, naturally infected with aster yellows, showing curved or twisted lateral flower stalks.



Plate 6.—Broccoli plants, grown for seed, naturally infected with aster yellows: A, profuse proliferation of the inflorescence, accompanied by phyllody, or the tendency of the floral organs to resemble leafy structures, and by virescence, or greening, of the flowers; B, enlarged leafy sepals, reduced petals, reduced or enlarged stamens, gynoeceium elongated and frequently club-shaped, and carpels often bifurcate. Lower right, cluster of abnormal flowers.



Plate 7.—Lettuce plants, grown for seed, naturally infected with aster yellows: *A*, upright or vertical branches, with secondary shoots rising from the axil of the leaves; *B*, curved or twisted branches; *C*, enlarged flower buds; *D*, normal flower buds and fruits with pappus of achenes protruding from a healthy plant.



Plate 8.—Leaves from carrot plants, grown for seed, naturally infected with aster yellows: *A*, chlorotic leaf with green midrib and lateral veins; *B*, margins of leaf purple instead of green; *C*, chicory plant, grown for seed, naturally infected with aster yellows, showing numerous axillary shoots, with the margin of the leaves undulating or wavy; sometimes the leaf is twisted into a corkscrew. The flower buds are dwarfed, fail to expand, and are surrounded by linear leafy structures.

ADDITIONAL ORNAMENTAL FLOWERING  
PLANTS NATURALLY INFECTED WITH  
CALIFORNIA ASTER YELLOWS

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# ADDITIONAL ORNAMENTAL FLOWERING PLANTS NATURALLY INFECTED WITH CALIFORNIA ASTER YELLOWS<sup>1</sup>

HENRY H. P. SEVERIN<sup>2</sup> and JULIUS H. FREITAG<sup>3</sup>

## INTRODUCTION

THE NATURAL infection of some ornamental flowering plants with California aster yellows has already been reported (Severin and Freitag, 1934).<sup>4</sup> In California, such infection was found on 8 species in 7 genera belonging to 4 families.

Severin (1942a, 1942b) described the symptoms, determined the incubation period of the disease, and reported on vectors of the aster-yellows virus on perennial delphinium and annual larkspur. A later paper (Severin, 1943) dealt with the disease on annual phlox (*Phlox Drummondii*), apparently the first case of a leafhopper-transmitted virus inducing breaking in color of flowers. In a companion paper the symptoms of this disease on vegetable and seed crops have been described (Severin and Frazier, 1945).

Surveys were made from 1934 to 1943 to determine additional host plants. Field investigations were conducted on the ranches of seed companies; on the University Farm at Davis; and in the canyons of the Montara Mountains, where the production of cut flowers is an important industry.

## METHODS

A detailed account on methods is given in the third paper of this series (Frazier and Severin, 1944).

## HOST RANGE OF VIRUS

The host range of the aster-yellows virus among ornamental flowering plants naturally infected includes 45 species and 1 interspecific hybrid in 38 genera belonging to 17 families, including those previously reported (Severin, 1929, 1942a, 1942b, 1943, Severin and Freitag, 1934). The season's duration of each plant is given in the following list:

### Boraginaceae:

*Myosotis scorpioides* L.,<sup>5</sup> true forget-me-not; annual or perennial

### Caryophyllaceae:

*Dianthus barbatus* L., sweet william; perennial

*Gypsophila paniculata* L.,<sup>\*</sup> baby's-breath; perennial

<sup>1</sup> Received for publication June 12, 1944.

<sup>2</sup> Entomologist in the Experiment Station.

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<sup>4</sup> See "Literature Cited" at the end of this paper for complete data on citations, referred to in the text by author and date of publication.

<sup>5</sup> Asterisk indicates overlapping host ranges of California and New York aster yellows viruses.

## Compositae:

- Chrysanthemum carinatum* L.,\* tricolor chrysanthemum; annual; variety Dwarfed Golden Queen  
*Chrysanthemum segetum* L., corn-marigold; annual; varieties Single Eldorado (Severin and Freitag, 1934) and Single Star  
*Chrysanthemum segetum* L.  $\times$  *C. carinatum* L., single yellow daisy; annual  
*Chrysanthemum frutescens* L.,\* Marguerite; perennial  
*Rudbeckia hirta* L.,\* black-eyed Susan; annual or biennial  
*Helianthus annuus* L., common garden sunflower; annual  
*Cosmos bipinnatus* Cav.,\* common cosmos; annual; varieties Giant Pink and White  
*Zinnia elegans* Jacq., common zinnia, annual; varieties Dahlia-flowered mixed, Double Giant Pink, and Lilliput Scarlet Gem (Severin and Freitag, 1934)  
*Coreopsis Drummondii* Torr. & Gray, golden wave coreopsis; annual  
*Coreopsis grandiflora* Nutt., bigflower coreopsis; annual  
*Brachycome iberidifolia* Benth.,\* Swan River daisy; annual  
*Callistephus chinensis* Nees,\* China aster (Severin, 1929); annual  
*Tagetes erecta* L.,\* African marigold (Severin and Freitag, 1934); annual  
*Tagetes patula* L., French marigold, dwarf type (Severin and Freitag, 1934); annual  
*Gaillardia pulchella* Foug. var. *Picta* Gray, gaillardia or blanket-flower; annual  
*Calendula officinalis* L.,\* pot-marigold; annual; varieties Lemon Queen and Winter Queen  
*Helichrysum bracteatum* Andr., strawflower (Severin and Freitag, 1934); annual  
*Centaurea americana* Nutt., basket-flower; annual  
*Centaurea Cyanus* L., cornflower or bachelor's button; annual

## Cruciferae:

- Cheiranthus Cheiri* L., wallflower; perennial

## Dipsaceae:

- Scabiosa atropurpurea* L.,\* mourning bride or sweet scabious; annual

## Labiatae:

- Salvia azurea* Lam. subsp. *Pitcheri* (Torr.) Epl., azure sage; perennial

## Onagraceae:

- Clarkia elegans* Dougl.,\* clarkia; annual  
*Godetia grandiflora* Lindl., godetia; annual; varieties Double Fairy Lady, Double Rosy Morn, Duke of York, semidwarfed Kelvedon Glory, Sybil Sherwood (Severin and Freitag, 1934), semidwarfed Sherwood, and Tall Single White Swan  
*Gaura Lindheimeri* Engelm. & Gray, white gaura; annual, biennial, or perennial

## Papaveraceae:

- Eschscholtzia californica* Cham.,\* California poppy (Severin and Freitag, 1934); annual or perennial

## Plumbaginaceae:

- Limonium sinuatum* Mill., sea-lavender; biennial or perennial; variety Rose Superba

## Polemoniaceae:

- Gilia capitata* Dougl., var. *achilleaefolia* (Benth.) Mason, globe gilia; annual  
*Phlox Drummondii* Hook.,\* Drummond phlox (Severin, 1943); annual

## Primulaceae:

- Primula polyantha* Mill., Polyanthus primrose; perennial

## Ranunculaceae:

- Ranunculus asiaticus* L., Turban and Persian buttercups (Severin and Freitag, 1934); perennial  
*Anemone coronaria* L., poppy-flowered anemone; perennial  
*Nigella damascena* L., love-in-a-mist; annual  
*Delphinium cultorum* Voss, perennial delphinium (Severin, 1942a); perennial  
*Delphinium Ajacis* L., rocket larkspur (Severin, 1942b); annual

## Rosaceae:

*Geum chilöense* Balb., geum; perennial

## Scrophulariaceae:

*Linaria bipartita* Willd., cloven-lip toadflax; annual

*Mimulus cardinalis* Dougl., crimson monkey-flower; perennial

*Mimulus guttatus* DC., common monkey-flower; annual or perennial

## Solanaceae:

*Petunia hybrida* Vilm.,\* petunia; annual; varieties Common, Dwarf Rose Bedder, Double Ruffled, Rosy Morn, Rosy Morn balcony-type

*Salpiglossis sinuata* Ruiz. & Pav., painted-glory; annual

## Tropaeolaceae:

*Tropaeolum majus* L., garden nasturtium; annual

## Umbelliferae:

*Trachymene caerulea* R. Graham,\* blue lace-flower; annual

In California the virus overwinters in the biennials and perennials and in the adult leafhoppers.

Previously noninfective short-winged aster leafhoppers, *Macrostelus divinus* (Uhl.), and long-winged aster leafhoppers, a race of the same species (Severin, 1940), recovered the virus from naturally infected plants and transferred it to healthy aster or celery plants. The short-winged aster leafhopper was transferred to healthy celery. The long-winged forms were placed on aster, because on celery they often would have died before the so-called "virus-incubation period" could be completed in them.

## SYMPTOMATOLOGY

The symptomatology of ornamental flowering plants naturally infected with aster yellows may vary according to the size of the plant when infected. Dwarfing is one noticeable symptom in which the degree of stunting depends upon the initial age of the plant. Shortening of the internodes is characteristic. One constant symptom is the production of axillary, leafy shoots from the bud normally dormant in the axil of each leaf. Another constant symptom is the upright or vertical position of the branches and leaves. Ornamental flowering plants naturally infected can be readily identified in the field by the compact, dense clusters of axillary, chlorotic shoots.

Among economic plants of the family Umbelliferae, curving, twisting, and intertwining of the petioles occur, as described for celery (Severin, 1929), celeriac (Severin and Frazier, 1944), carrots, parsley, and parsnips (Severin, 1932). Thus far these symptoms have not been found on any naturally infected ornamental flowering plant.

The foliage symptoms vary among different species of flowering ornamentals. The first symptom on aster, sea lavender, petunia, salpiglossis, mourning bride, and marigold is a clearing of the veins and veinlets, with a faint yellow vein-banding on the youngest leaves. In most ornamental flowering plants this does not appear. The leaves of infected plants may show an inward or outward rolling of the margin, an inward or outward cupping, a twist or spiral along the long axis, and malformation; often they are asymmetrical.

The most striking symptoms on the flowers of some ornamental plants are phyllody, the tendency of the floral organs to resemble leafy structures; virescence or the greening of the flowers; and proliferation of the flowers.

#### BORAGINACEAE, BORAGE FAMILY

True forget-me-not (*Myosotis scorpioides*): Infected plants produce numerous upright, axillary shoots with linear leaves. A noticeable symptom is the reddening of the lower leaves while the upper leaves are chlorotic. The flowers are abnormal, dwarfed, green, and densely clustered, sometimes on long pedicels (fig. 1, A, B).



Fig. 1.—True forget-me-not (*Myosotis scorpioides*): A, apical shoot showing dense clusters of abnormal, dwarfed, virescent flowers; B, shoot showing flowers on long pedicels (Salinas, August 20, 1940).

#### CARYOPHYLLACEAE, PINK FAMILY

Sweet william (*Dianthus barbatus*): Plants are stunted; internodes shortened (plate 1, C); stems twisted and deformed; axillary shoots dwarfed, twisted, and chlorotic (plate 1, C). Young leaves are yellow and cupped inward toward the midrib (plate 1, C); flower buds are reduced; bracts are stiff and upright; sometimes the bud dries prematurely.

Baby's-breath (*Gypsophila paniculata*): Naturally infected plants are stunted, with numerous axillary shoots that form dense clusters (plate 2, C). Virescence, phyllody, and proliferation of the flowers occur (plate 2, B). The calyx is enlarged (plate 2, B), and the petals are reduced (plate 2, C).

#### COMPOSITAE, COMPOSITE FAMILY

Tricolor Chrysanthemum (*Chrysanthemum carinatum*): Infected plants of the Dwarf Golden Queen variety are stunted, with curved stems; the compact clusters of axillary shoots have dwarfed, green flower buds; flowers are

sessile and green, frequently have few or no rays, and are surrounded by a rosette of chlorotic leaves with curved petioles.

Corn-marigold (*Chrysanthemum segetum*): The symptoms on infected

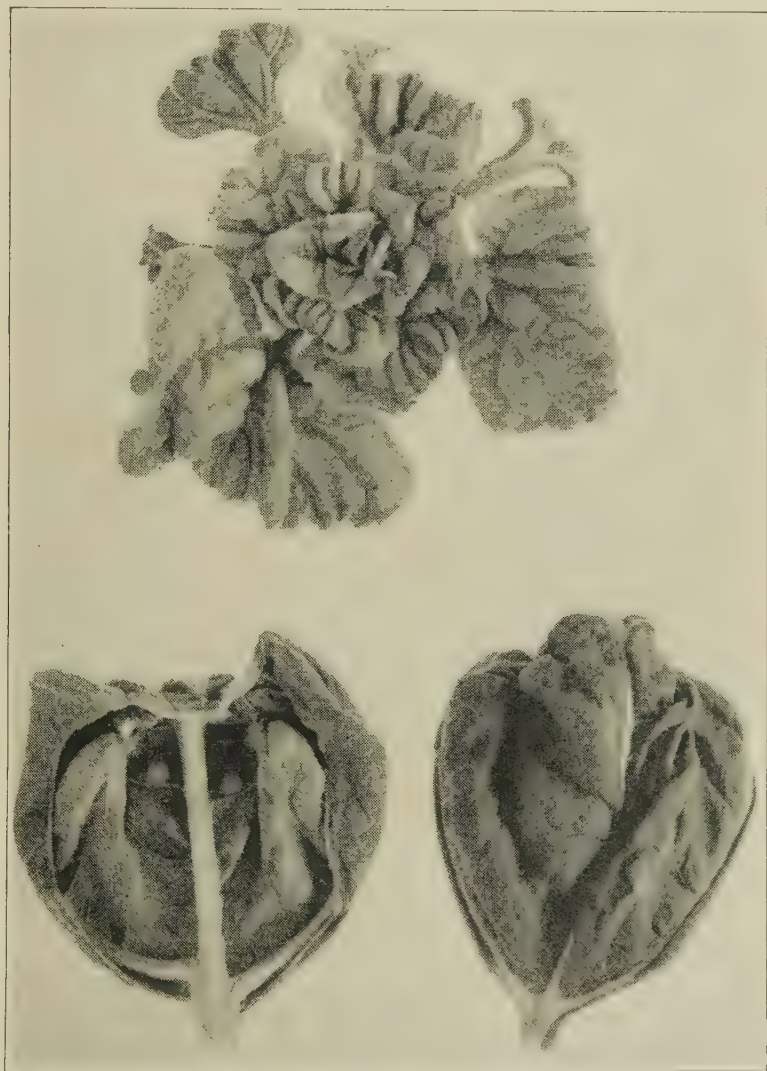


Fig. 2.—Common sunflower naturally infected with aster yellows: upper, cluster of chlorotic, outward-cupped leaves on the apical end of the branch; lower, extreme inward cupping of leaves, resembling a ball.

plants of the Single Eldorado and Single Star varieties are similar to those just described (plate 2, D).

Single yellow daisy, an interspecific hybrid with characters of *Chrysanthemum segetum* predominating, but with winged achenes of *C. carnatum*: The symptoms resemble those on tricolor chrysanthemum. Axillary flower buds

are sessile or they have short peduncles which are surrounded by curved or twisted leaves (plate 3, *A*).

Marguerite (*Chrysanthemum frutescens*): Sometimes infected plants show symptoms on one branch or a portion of the plant and the remainder appears normal. In plants seriously affected, the internodes are so shortened that a rosette of extremely dwarfed leaves is formed. The axillary shoots are dwarfed and rosetted; older leaves are chlorotic along the margin; younger leaves roll outward toward the petiole and are yellow. No floral abnormality was observed. The yellow variety seemed to be more susceptible than the white.

Black-eyed Susan (*Rudbeckia hirta*): Infected plants are dwarfed and chlorotic; they produce malformed, virescent flowers.

Common sunflower (*Helianthus annuus*) in the Castro Valley was proved to be naturally infected with aster yellows. Infected plants were dwarfed, with bunches of chlorotic, outward-cupped leaves on the apical ends of the branches (fig. 2). The cupping sometimes continues until each bunch resembles a ball (fig. 2).

Common cosmos (*Cosmos bipinnatus*): Infected plants of the Giant Pink and White varieties are stunted, with chlorotic apical and axillary shoots; stems are curved, and the leaves often curl down; flowers are dwarfed and green, with petals reduced or lacking (plate 3, *F*).

Golden-wave coreopsis (*Coreopsis Drummondii*): Infected plants are stunted; internodes and peduncles are shortened; dwarfed axillary shoots develop from the axillary buds, producing flowers with shortened peduncles; leaves of the axillary shoots are reduced and tinged with yellow along the margin and commonly with red; flowers are abnormal, yellowish green; involucre bracts usually are enlarged; ray flowers are reduced and dry; disk flowers are transformed into a complete new composite head, which is sometimes repeated to three series; the bracts of receptacle are much enlarged, green, and linear; and the achene portion of normal flower becomes elongated into a peduncle.

Bigflower coreopsis (*Coreopsis grandiflora*): Axillary shoots of infected plants are dwarfed; stems, petioles, and young leaves are chlorotic; pedicels are chlorotic, somewhat shortened, and occasionally twisted, sometimes slightly curved; involucre bracts are somewhat reduced and flattened outward, with cleared venation; the involucre is green and loosely opened; individual flowers show phyllody; achenes are greatly elongated to form a flattened pedicel, bearing a complete minute, green, composite flower with a complete series of involucre bracts; floral bracts are enlarged and linear, and dry early; petals are somewhat reduced and dry; stamens unaffected; bracts of receptacle elongated, enlarged, and leaflike; ray flowers reduced, green, and leafy.

Swan River daisy (*Brachycome iberidifolia*): Infected plants are stunted and chlorotic, with thin, axillary shoots; leaves are dwarfed, and flower buds yellowish.

Gaillardia, or blanket-flower (*Gaillardia pulchella* var. *picta*): Healthy plants grow 12 to 20 inches high; but infected plants are dwarfed, with chlorotic, upright leaves. Virescence of the flowers occurs.

Pot-marigold (*Calendula officinalis*): Plants shown to be naturally infected with aster yellows are stunted. On the Lemon Queen variety, veins and vein-

lets are clear, with yellow veinbanding on the youngest leaves (plate 4, *C*); flowers and flower buds are dwarfed and green (plate 2, *E*). On the Winter Queen variety the symptoms are short, chlorotic, axillary shoots having thick, dwarfed, curled leaves; flower buds are green.

Basket-flower (*Centaurea americana*): Infected plants are stunted, chlorotic, with numerous axillary shoots, which frequently have dwarfed, curved leaves; flowers are often reduced and fail to expand.

Cornflower, or bachelor's-button (*Centaurea Cyanus*): Infected plants are stunted, the stems spindling and upright; enormous numbers of axillary



Fig. 3.—Wallflower (*Cheiranthus Cheiri*): *A*, shoot from a healthy plant showing normal flowers; *B*, *C*, shoots from naturally infected plants, showing flower organs replaced by green, leafy, orbicular structures, with long peduncles (Union Island, May 1, 1929).

shoots produce a broomlike appearance; flower production is inhibited; flower buds are very small, almost vestigial, and become dry and scarious before expanding.

#### CRUCIFERAE, MUSTARD FAMILY

Wallflower (*Cheiranthus Cheiri*): The most noticeable symptoms are virescence, phyllody (fig. 3, *B*, *C*), and proliferation of the flowers. Proliferated flowers often terminate in green, orbicular, leafy structures.

#### DIPSACEAE, TEASEL FAMILY

Mourning bride (*Scabiosa atropurpurea*): Plants are stunted (plate 5, *D*), with the main and floral stems and peduncles twisted and occasionally curling; the axillary shoots bear dwarfed, chlorotic leaves (plate 3, *D*); virescence and phyllody of the flowers occur; the calyx and corolla tube are elongated; enlargement of the flowers produces a long, loose flower head (plate 3, *C*, *E*).

**LABIATAE, MINT FAMILY**

Azure sage (*Salvia azurea* subsp. *Pitcheri*) : The apical shoots are chlorotic; the axillary shoots bear linear, chlorotic leaves.

Petunia (*Petunia hybrida*) : Dwarf Rose Bedder, Double Ruffled, Common, Rosy Morn, and Rosy Morn balcony-type, all were found to be naturally infected. Plants are stunted, with shortened internodes; axillary shoots are dwarfed and chlorotic, with twisted stems; young leaves are dwarfed, chlorotic, and cupped inward (plate 5, *C*), and show cleared venation banded with green; older leaves are bronzed along the margin and basal portion, and cupped outward; flowers are reduced, corolla tube and petals are often green (plate 5, *C*), and frequently the corolla is withered and dry. Infected plants are often deep green, but in the later stages turn yellow.

**ONAGRACEAE, EVENING-PRIMROSE FAMILY**

Clarkia (*Clarkia elegans*) : Infected plants are stunted, with upright branches and chlorotic, apical, and reddened lower leaves; virescence, phyllody, and proliferation of the flowers occur.

Godetia (*Godetia grandiflora*) : Double Fairy Lady, Double Rosy Morn, Duke of York, semidwarfed Kelvedon Glory, Sybil Sherwood, Tall Single White Swan varieties were found to be infected. Plants are chlorotic, with clusters of axillary shoots at the apical ends of the branches; leaves are dwarfed and curl downward; flowers frequently are green; sepals and petals are sometimes dwarfed and chlorotic; the petals may be absent; flower buds may become dry and fail to expand.

White gaura (*Gaura Lindheimeri*) : The virus was recovered from infected plants.

**PLUMBAGINACEAE, PLUMBAGO OR LEADWORT FAMILY**

Sea-lavender (*Limonium sinuatum*) : Infected plants of the variety Rose Superba are stunted, with upright leaves and numerous chlorotic axillary shoots (plate 5, *A*); youngest leaves show clearing of the veins (plate 4, *A*); the older leaves are reddened and cupped inward, with the petioles bent down (plate 5, *A*); the flowers are dwarfed, malformed, and virescent.

**POLEMONIACEAE, PHLOX FAMILY**

Globe gilia (*Gilia capitata* var. *achilleaefolia*) : Naturally infected plants are chlorotic, with the axillary shoots dwarfed, curved, twisted, and spindling; the leaves reduced and chlorotic; the pinnules needlelike, tending to assume an upright position. Flowers are placed individually along a very loose umbel-like floral branch; they may have long peduncles instead of forming dense, globose, headlike clusters as in healthy plants; they are usually reduced and green, and often the buds dry prematurely.

**PRIMULACEAE, PRIMROSE FAMILY**

Polyanthus primrose (*Primula polyantha*) : Infected plants are stunted, with numerous axillary shoots; leaves are yellow, and the youngest leaves linear; the flowers are green, with shortened peduncles (plate 4, *D*).

**RANUNCULACEAE, CROWFOOT FAMILY**

Poppy-flowered anemone (*Anemone coronaria*): Plants are stunted and chlorotic. The youngest leaves are dwarfed, with shortened petioles; sometimes the blades are reduced to small, curved, clublike expansions of the petioles. The older leaves are chlorotic and curl outward. Virescence (greening) of both single and double flowers is common, with a rosette of involueral bracts below the flowers (plate 4, B).

Love-in-a-mist (*Nigella damascena*): Infected plants develop dense clusters of axillary shoots (plate 5, B). The smaller plants have dwarfed, chlorotic leaflets; the larger ones bear a tuft of axillary shoots at the apical end of the branches, and often their flower buds fail to expand.

**ROSACEAE, ROSE FAMILY**

Geum (*Geum chiloense*): Plants naturally infected with aster yellows develop dwarfed, chlorotic shoots from the crown, with spindling, chlorotic leaves that show slightly cleared venation. On affected blossom-bearing shoots the flowers are dwarfed, the petals green and leaflike, the stamens often reduced, the sepals enlarged and leafy, and the peduncles chlorotic.

**SCROPHULARIACEAE, FIGWORT FAMILY**

Cloven-lip toadflax (*Linaria bipartita*): The virus was recovered by previously noninfective long-winged aster leafhoppers and transferred to asters. No notes were taken on the symptoms.

Crimson monkey-flower (*Mimulus cardinalis*): The basal stems of the plant are affected; internodes are shortened; tips of affected stems and axillary shoots are stunted and chlorotic; the apical part of the plant shows no symptoms; the leaves are dwarfed and chlorotic.

Common monkey-flower (*Mimulus guttatus*): The virus was recovered from infected plants by short-winged and long-winged aster leafhoppers and transferred to healthy aster or celery. The symptoms were not recorded.

**SOLANACEAE, NIGHTSHADE FAMILY**

Painted-glory (*Salpiglossis sinuata*): Infected plants are dwarfed, with chlorotic, axillary shoots; petioles are often bent downward; leaves are cupped inward and sometimes show clear veins and veinlets.

**TROPAEOLACEAE, TROPAEOLUM FAMILY**

Garden nasturtium (*Tropaeolum majus*): Young infected plants assume an upright habit of growth, with cupped leaves; internodes of older plants are shortened; younger leaves and buds are minute near the apical end of the stems; axillary shoots are dwarfed and chlorotic, with curved or twisted stems; older leaves are reduced and cupped inward, with margins rolled inward; petioles are elongated; virescence and phyllody of the flowers occur (fig. 4); the calyx is sometimes reduced; the petals are cupped, leafy structures at the apical ends of flattened stalks (fig. 4); the stamens are often elongated, and are sometimes vestigial; and the gynoecium is enlarged and club like (fig. 4).

## UMBELLIFERAE, PARSLEY FAMILY

Blue lace-flower (*Trachymene caerulea*): Infected plants are stunted and chlorotic; peduncles are shortened and curved (plate 6, *B*), with apical stems bearing dwarfed green flowers; the axillary shoots (plate 6, *A*) have rosettes of leaves, often purple, below the virescent flowers (plate 6, *E*); pedicels are elongated, and the petals cupped inward (plate 6, *D*); often the flower buds become dry and fail to expand.



Fig. 4.—Garden nasturtium (*Tropaeolum majus*): flowers showing phyllody, the replacement of flower parts with leaflike structures; carpels greatly elongated, and flowers green (Salinas, August 16, 1939).

HOST-RANGE DIFFERENCES OF CALIFORNIA AND  
NEW YORK ASTER YELLOWS

Garden nasturtium (*Tropaeolum majus*), of the family Tropaeolaceae, was naturally infected with California aster yellows. Neither this nor any other species of this family was listed by Kunkel (1931) as a host of the New York aster yellows. *Zinnia elegans* was shown to be naturally infected with the California aster-yellows virus, but according to Kunkel (1931) the New York aster-yellows virus was not transmitted to this species of flowering plant.

Kunkel (1926-1931) reported for the virus of New York aster yellows a host range including 184 species in 151 genera belonging to 38 families. Among ornamental flowering plants 168 species were experimentally infected, but only 6 species were found to be naturally attacked. The viruses of California and New York aster yellows have overlapping host ranges that include 15 species in 9 families, indicated by asterisks in the list (pages 599-601).

## SUMMARY

Among ornamental flowering plants in California, 45 species and 1 inter-specific hybrid in 36 genera belonging to 17 families have been shown to be naturally infected with aster yellows. Previously noninfective short-winged and long-winged aster leafhoppers recovered the virus from the naturally infected plants and transferred it to healthy aster or celery.

The symptoms on flowering ornamentals naturally infected vary according to the size of the plant when infected. Noticeable symptoms include stunting; shortening of the internodes; production of axillary shoots from the bud normally dormant in the axil of each leaf; upright or vertical position of the leaves and stems; cleared venation; cupping, twisting, and chlorosis of the leaves. The most striking symptoms are phyllody, the tendency of the floral organs to resemble leafy structures; virescence of the flowers; and proliferation of the flowers.

## ACKNOWLEDGMENT

We are indebted to Dr. H. L. Mason and the late Miss Ethel Crum, Botany Department, University of California, for determining the species and varieties of ornamental flowering plants.

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PLATES





Plate 1.—A, B, Sea-lavender (*Limonium sinuatum*), Rose Superba variety: A, shoot from a healthy plant; B, shoot from a diseased plant, showing basal upright, chlorotic leaves and dwarfed, abnormal, green flowers. C, sweet william (*Dianthus barbatus*): apical branch showing shortened internodes, twisted stems, and deformed, twisted, chlorotic, axillary shoots bearing yellow leaves cupped inward toward the midrib (Montara, August 9, 1934).



Plate 2.—A-C, Baby's-breath (*Gypsophila paniculata*): A, shoots from healthy plant with normal flowers; B, shoots from infected plant, showing dwarfed green flowers with enlarged calyxes; C, stem from diseased plant with numerous axillary shoots bearing abnormal, green flowers and elongated sepals, petals, and pistils (Montara, October 13, 1936). D, Corn-marigold (*Chrysanthemum segetum*): center, normal flower; grouped around it, four dwarfed, green flowers, ray florets reduced or lacking (Montara, November 8, 1934). E, Pot-marigold (*Calendula officinalis*), Lemon Queen variety: center, normal flower; grouped around it, six dwarfed abnormal, green flowers (Montara, August 9, 1934).



Plate 3.—A, Single yellow daisy (*Chrysanthemum segetum* × *C. carinatum*): branch showing axillary, sessile flower buds, or short peduncles surrounded by curved or twisted leaves (Montara, November 8, 1934). B—E, Mourning bride (*Scabiosa atropurpurea*): B, normal flowers from healthy plant; C, E, abnormal flowers with pedicels elongated; D, apical, chlorotic flower head (Montara, September 24, 1935). F, Common cosmos (*Cosmos bipinnatus*), Giant Pink variety: center, normal flower from healthy plant; grouped around it, six dwarfed, green flowers with or without petals (Montara, July 31, 1934).



Plate 4.—A, Sea-lavender (*Limonium sinuatum*), Rose Superba variety: youngest leaf, showing clearing of the veins (San Bruno, April 19, 1944). B, Poppy-flowered anemone (*Anemone coronaria*): left, single and double flowers from healthy plants; right, virescence or greening of single and double flowers with rosettes of involucre bracts below the flowers (Half Moon Bay, November 8, 1934). C, Pot-marigold (*Calendula officinalis*), Lemon Queen variety: left, leaf showing cleared venation; right, leaf from healthy plant (Montara, August 9, 1934). D, Polyanthus primrose (*Primula polyantha*): left, cluster of flowers from a healthy plant; right, green flowers with shortened peduncles (Montara, October 13, 1936).



Plate 5.—A. Sea-lavender (*Limonium sinuatum*), Rose Superba variety: apical branch showing axillary shoots; older leaves cupped inward, and petioles bent down (Montara, September 24, 1935). B. Love-in-a-mist (*Nigella damascena*): two plants showing dense clusters of axillary shoots (Half Moon Bay, October 13, 1936). C. Petunia (*Petunia hybrida*), Rosy Morn balcony type: virescent flowers, mostly with sepals but no corolla tube (Salinas, July 28, 1943). D. Mourning bride (*Scabiosa atropurpurea*): stunted plant with apical and axillary chlorotic shoots (Montara, September 24, 1934).



Plate 6.—Blue lace-flower (*Trachymene caerulea*): *A*, apical stem with axillary shoots bearing dwarfed, green flowers; *B*, curved peduncles; *C*, normal flower from healthy plant; *D*, abnormal flower with elongated pedicels; *E*, rosette of leaves below virescent flowers (Montara, November 8, 1934).

WEED-HOST RANGE OF CALIFORNIA  
ASTER YELLOWS

NORMAN W. FRAZIER AND HENRY H. P. SEVERIN



# WEED-HOST RANGE OF CALIFORNIA ASTER YELLOWS<sup>1</sup>

NORMAN W. FRAZIER<sup>2</sup> AND HENRY H. P. SEVERIN<sup>3</sup>

## INTRODUCTION

KUNKEL (1926, 1931)<sup>4</sup> recorded for the virus of New York aster yellows an extensive host range of 184 species of plants in 151 genera belonging to 38 families. He found 12 species of naturally infected weeds in 4 families, as follows:

Compositae, composite family:

- Horseweed, *Erigeron canadensis* L.
- Erigeron speciosus* (Lindl.) DC.
- Galinsoga, *Galinsoga parviflora* Cav.
- Helenium autumnale* L.
- Helenium nudiflorum* Nutt.
- Fall dandelion, *Leontodon autumnalis* L.
- Black-eyed Susan, *Rudbeckia hirta* L.
- Perennial sow thistle, *Sonchus arvensis* L.
- Common sow thistle, *Sonchus oleraceus* L.

Plantaginaceae, plantago family:

- Common plantain, *Plantago major* L.

Rosaceae, rose family:

- Rough cinquefoil, *Potentilla monspeliensis* L.

Umbelliferae, parsley family:

- Wild carrot, *Daucus Carota* L.

Ogilvie (1927a, 1927b) reported aster yellows (strain not specified) to be common in the Bermuda Islands and observed that several wild plants were affected, the commonest being common sow thistle, *Sonchus oleraceus*.

Severin (1929, 1938) determined the following 2 species to be hosts of the California aster-yellows virus:

Plantaginaceae, plantago family:

- Common plantain, *Plantago major* L.

Umbelliferae, parsley family:

- Poison hemlock, *Conium maculatum* L.

Thompson (1944) tested 16 species of wild *Lactuca* and 6 additional strains for their susceptibility to New York aster yellows under field conditions. He reported that the following 13 species showed symptoms: *Lactuca altaica* Fisch. and Mey., *L. canadensis* L., *L. floridana* (L.) Gaertn., *L. graminifolia*

<sup>1</sup> Received for publication May 19, 1944.

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<sup>4</sup> See "Literature Cited" at the end of this paper for complete data on citations, referred to in the text by author and date of publication.

Michx., *L. indica* L., *L. muralis* (L.) Fresen., *L. perennis* L., *L. raddeana* Maxim., *L. saligna* L., *L. serriola* L., *L. spicata* (Lam.) Hitchc., *L. Squarrosa* (Thunb.) Miq., and *L. virosa* L. Three species, *L. Bourgaei* (Boiss.) Irish and Taylor, *L. Marschalli* Stebbins, and *L. tatarica* (L.) C. A. Mey., failed to develop symptoms, and Thompson concluded that they seemed to be immune to the virus.

In two companion papers the symptoms of the disease on vegetable and seed crops, and ornamental flower plants have been described (Severin and Frazier, 1945; Severin and Freitag, 1945).

Field investigations were conducted from 1928 to 1944 to determine additional weed-host plants of this virus. Attempts were made to recover the virus from naturally infected weeds. Experiments were also conducted in the greenhouse to ascertain what weeds were susceptible to the virus, and attempts were made to recover the virus. The longevity of the last living male of 4 vectors was ascertained on the inoculated weeds, and a record was kept of all plants on which the vectors completed their life cycle. A study of the symptoms of the disease was undertaken on both naturally infected and experimentally infected weeds.

## MATERIALS AND METHODS

*Weeds.*—Weed seedlings were collected in the field or grown from seeds; and 10 or more plants of each species were planted in 6-inch clay pots, 8 plants to be inoculated and the remaining 2 or more to serve as controls. These controls were used to test the possibility of encountering plants that were infected in the field before being collected, and also of subsequent accidental infection in the greenhouse. They were used also in comparisons of the symptoms that appeared on the infected plants of the same species. The seedlings chosen were apparently free from all diseases. Since the plants were allowed enough time after potting—usually 3 weeks or more—to develop size and vigor for withstanding insects confined on them, there was very slight possibility of using any plant previously infected. Not a single case of aster yellows developed on weed seedlings collected in the field unless they had subsequently been placed in a cage with infective leafhoppers.

All plants were kept in one greenhouse except during the time that insects were confined on them in a second greenhouse about 120 feet away. Accidental infection of any plant with aster yellows has never been observed in the first greenhouse. The insects were maintained in the second greenhouse, and all operations involving their transfer were carried on in a headhouse separate from both greenhouses. Inoculated plants were kept under observation either until after flowering or until they died. Most plants developing symptoms were observed until their death in order to obtain a complete picture of the disease at all stages. Often this period exceeded 8 months, one yellowed plant being under observation for more than 16 months.

*Vectors.*—Parallel inoculation tests were made with 4 leafhopper vectors of proved ability to transmit the virus of California aster yellows. Infective populations of the mountain leafhopper, *Colladonus montanus* (V.D.) = (*Thamnotettix montanus* V.D.), and the geminate leafhopper, *Idiodonus geminatus* (V.D.) = (*T. geminatus* V.D.), were maintained on either natu-

rally or experimentally infected celery plants, on which both species readily reproduced. Infected asters were used to perpetuate infective populations of both the short-winged leafhopper, *Macrostelus divisus* (Uhl.), and the long-winged aster leafhopper, a race of the same species (Severin, 1940).

*Experimental Infection.*—Infective insects were used in experiments to determine the ability of the 4 leafhoppers to complete their life cycle on all the weed species tested, as well as in experiments to determine the longevity of the males under those same conditions. Separate lots of 20 male and 20 female leafhoppers of each of the 4 vectors were confined to a single plant of each weed species, making a total of 8 plants that were subjected to experimental infections by all 4 vectors.

*Recovery of Virus from Experimentally Infected Weeds.*—Populations of noninfective short-winged and long-winged aster leafhoppers were maintained on Sacramento barley, a plant immune to aster yellows (Severin, 1929). Both vectors were used to recover the virus from experimentally infected weeds and transfer it to healthy asters. Twenty-five previously noninfective males, confined on each infected weed, were allowed to feed for 1 to 7 days, the time depending upon their ability to survive on different weed species. They were then removed from the weed and confined on a healthy aster plant for 30 days, to allow ample time for completion of the so-called "incubation period" of the virus in the insect. The leafhoppers were then removed, and the aster was placed in an insectproof cage, where it was observed until it was past the flowering stage or until it had shown reliable symptoms of aster yellows. Male leafhoppers were used in order to avoid egg deposition in the asters; otherwise nymphs hatched from eggs would have provided a source of accidental infection in insectproof cages where such asters were kept after removal of the insects.

Repeated attempts were often made to recover the virus from one or more plants of each species of weed, but one successful transfer of the virus to aster from any weed species was considered proof of the susceptibility of that species.

*Recovery of Virus from Naturally Infected Weeds.*—The procedure to recover the virus from plants naturally infected with aster yellows was almost the same as the method described above for recovering the virus from plants experimentally infected. There was, however, one difference: the naturally diseased plants, or portions therefrom, were placed in jars of water to keep them fresh. In order to confine previously noninfective insects on such plants, the stems or roots were pulled through a hole cut in the center of a piece of cardboard. The cardboard, placed on the top of a jar of water, acted as a platform upon which the insect cage was placed; and the hole, meanwhile, allowed the roots or stems of the plants to extend into the water. This is the technique described by Severin and Freitag (1934).

## LIFE CYCLE AND LONGEVITY OF FOUR VECTORS

*Completion of Life Cycle.*—Experiments were conducted to determine whether each of the 4 vectors could complete its egg and nymphal stages on each weed species. Lots of 20 infective females of each vector oviposited in healthy weeds for 3 to 5 days, depending upon the size of the plant and upon

the season. Egg deposition, on the average, is greater in summer than in winter. As a rule, the shorter period of confinement was used during the summer to avoid producing undesirably high populations of nymphs. After removal of the cage containing the females, an empty cage was placed over the plant. Daily observations were made on the emergence and longevity of the nymphs, and on their completion or noncompletion of the nymphal stages. Immediately after one or two nymphs had become adults, all insects were removed from the plant to prevent egg deposition. The plant, fumigated with "Nico-fume" tobacco-paper insecticide, was then returned to the first greenhouse, where daily observations were continued with respect to infection.

Table 1 shows the plants on which leafhoppers attained the adult stage. The leafhoppers would probably have been able to reach maturity on additional weed species if further trials had been made. In several instances tests were incomplete owing to the premature death of the plant while nymphs were still alive and sometimes in the last nymphal stage. Furthermore, weeds at the time of being caged with the insects varied in size and vigor; and an occasional plant suffered from populations of red spider, which multiplied rapidly on certain species of weeds under cage conditions. Any one of these factors could conceivably influence the results of the test and may constitute a source of error which, because single trials were made, cannot be reduced or evaluated. For these reasons, though the positive results contained in table 1 are valid, the negative results cannot be regarded as reliably significant; additional trials might yield different results with some species.

Often, on unfavorable host plants, nymphs emerged from eggs but soon died. On some plants only a very few of those hatching reached the adult stage. On more favorable host plants higher percentages survived and became adults. Nymphs were hatched from eggs of at least 1 of the 4 vectors on all weed species except *Eremocarpus setigerus*, and attained the adult stage on 50 of the 67 weeds.

Under greenhouse conditions, each of the 4 vectors can complete its nymphal stages on a rather wide range of weeds. In this respect the short-winged aster leafhopper is perhaps more restricted than the other 3 vectors. *Colladonus montanus* and *Idiodonus geminatus* seem slightly more adapted to weeds than the 2 aster-leafhopper vectors. In only 1 weed family was there any marked difference in the host-plant relations between the genera of leafhoppers. In the family Chenopodiaceae, *C. montanus* and *I. geminatus* completed their nymphal stages on 4 of the 6 species tested, but neither the short-winged nor the long-winged aster leafhopper was able to attain the adult stage on any of them.

*Longevity of Males.*—A comparison was made of the ability of each of the 4 vectors to survive on the 67 species of weeds tested. Lots of 20 infective males of each vector, confined in cages on healthy plants, were allowed to remain until the last insect of each lot had died, as determined by daily examinations. Then, after the cages had been removed, the plants were fumigated and returned to the first greenhouse for continued observation in regard to symptoms. Table 1 gives results of this experiment.

As in the experiments on life cycle, only single tests were made with each vector on each species of weed. Several tests may be regarded as incomplete

TABLE 1  
LONGEVITY OF MALES AND COMPLETION OF LIFE CYCLE ON WEEDS\*

Family, scientific, and common name of plant	Short-winged aster leafhopper		Long-winged aster leafhopper		<i>Colladonus montanus</i>		<i>Idionotus geminatus</i>	
	Lon- gevity	Life cycle	Lon- gevity	Life cycle	Lon- gevity	Life cycle	Lon- gevity	Life cycle
	days		days		days		days	
Amaranthaceae								
<i>Amaranthus retroflexus</i> L., rough pig-weed.....	7	C	10	—	25	C	33	—
Boraginaceae								
<i>Heliotropium curassavicum</i> L., alkali heliotrope.....	10	—	16	—	57	—	28	C
Caryophyllaceae								
<i>Stellaria media</i> (L.) Cyr., common chickweed.....	15	—	17	—	38	—	46	—
<i>Spergula arvensis</i> L., corn spurry.....	37	—	20	—	48	C	53	C
Chenopodiaceae								
<i>Chenopodium album</i> L., lamb's-quarters.....	8	—	18	—	29	C	20	C
<i>Chenopodium murale</i> L., nettle-leaf goosefoot.....	12	—	12	—	15	C	3	—
<i>Chenopodium ambrosioides</i> L., Mexican tea.....	8	—	11	—	36	C	20	C
<i>Atriplex patula</i> L., spear orache.....	10	—	10	—	29	C	75	C
<i>Atriplex rosea</i> L., redscale.....	10	—	7	—	7	—	11	C
<i>Salsola Kali</i> L. var. <i>tenuifolia</i> G.F.W. Mey, Russian thistle.....	10	—	7	—	7	—	14	—
Compositae								
<i>Hypochoeris radicata</i> L., hairy cat's-ear.....	11	—	9	—	4	C	12	—
<i>Lactuca Scariola</i> L. var. <i>integrata</i> Gren. & Godr., prickly lettuce.....	22	—	10	—	6	—	x	—
<i>Sonchus oleraceus</i> L., common sow thistle.....	50	—	15	—	6	C	8	—
<i>Erigeron linifolius</i> Willd., flax-leaved fleabane.....	70	C	110	C	12	—	72	C
<i>Taraxacum vulgare</i> (Lam.) Schrank., common dandelion.....	14	—	57	C	6	—	15	C
<i>Grindelia camporum</i> Greene, gum plant.....	11	—	56	—	5	C	7	C
<i>Heterotheca grandiflora</i> Nutt., telegraph plant.....	13	—	8	—	5	C	7	C
<i>Aster chilensis</i> Nees, common aster.....	45	C	7	C	x	—	x	C
<i>Gnaphalium decurrens</i> Ives var. <i>californicum</i> Gray, California everlasting.....	59	—	7	—	35	C	7	—
<i>Helianthus californicus</i> DC., California sunflower.....	x	—	x	—	x	—	x	C
<i>Madia sativa</i> Molina, Chilean tarweed.....	9	C	71	—	59	—	45	—
<i>Xanthoxylum spinosum</i> L., spiny clotbur.....	28	C	65	C	15	C	10	C
<i>Anthemis Cotula</i> L., mayweed.....	20	C	10	—	30	—	45	C
<i>Achillea millefolium</i> L. var. <i>lanulosa</i> Piper, milfoil.....	51	—	48	—	72	—	80	—
<i>Matricaria suaveolens</i> (Pursh) Buch., pineapple weed.....	62	C	40	C	78	C	78	C
<i>Cotula australis</i> Hook., Australian brass buttons.....	55	—	39	—	39	—	55	—
<i>Centaurea melitensis</i> L., Napa thistle.....	24	C	22	—	14	—	24	—
<i>Centaurea Cyanus</i> L., cornflower.....	36	—	35	—	72	—	28	—
Convolvulaceae								
<i>Convolvulus arvensis</i> L., wild morning-glory.....	16	—	11	C	5	—	7	—
Cruciferae								
<i>Brassica campestris</i> L., common yellow mustard.....	18	—	41	C	67	—	35	—
<i>Lepidium Draba</i> L., hoary cress.....	9	—	9	—	14	—	21	—
Dipsacaceae								
<i>Dipsacus fullonum</i> L., fuller's teasel.....	13	—	8	C	28	C	13	C
Euphorbiaceae								
<i>Eremocarpus setigerus</i> Benth., turkey-mullein.....	3	—	2	—	3	—	3	—
<i>Euphorbia Peplus</i> L., petty spurge.....	23	—	34	—	96	—	137	C
Geraniaceae								
<i>Geranium dissectum</i> L., cut-leaved geranium.....	37	C	29	C	49	C	35	C
<i>Erodium moschatum</i> L'Her., whitestem filaree.....	60	C	60	C	49	C	35	C
Hypericaceae								
<i>Hypericum perforatum</i> L., Klamath weed.....	9	—	11	—	8	—	12	—

\* Explanation of symbols given at end of table on next page.

TABLE 1—Continued\*

Family, scientific, and common name of plant	Short-winged aster leafhopper		Long-winged aster leafhopper		<i>Colladonus montanus</i>		<i>Idiodonus geminatus</i>	
	Lon- gevity	Life cycle	Lon- gevity	Life cycle	Lon- gevity	Life cycle	Lon- gevity	Life cycle
	days		days		days		days	
<b>Labiatae</b>								
<i>Marrubium vulgare</i> L., horehound.....	12	—	10	—	—	—	12	—
<i>Stachys bullata</i> Benth.....	7	—	x	—	x	—	13	x
<i>Lamium amplexicaule</i> L., dead nettle....	7	—	40	—	46	—	25	—
<b>Leguminosae</b>								
<i>Melilotus alba</i> Desr., white sweetclover..	16	—	9	C	—	C	—	C
<i>Lotus salusuginosus</i> Greene.....	14	C	9	—	133	C	35	C
<b>Malvaceae</b>								
<i>Malva nicaeensis</i> All., bull mallow.....	92	C	85	C	38	C	44	—
<i>Sida hederacea</i> (Dougl.) Torr., alkali mallow.....	12	—	10	—	7	—	69	—
<b>Onagraceae</b>								
<i>Epilobium californicum</i> Hausskn., willow herb.....	60	C	9	—	16	—	9	—
<i>Epilobium paniculatum</i> Nutt., panicle willow herb.....	124	C	22	C	122	C	113	C
<b>Oxalidaceae</b>								
<i>Oxalis rubra</i> A. St. Hill.....	7	—	11	C	12	—	31	—
<b>Plantaginaceae</b>								
<i>Plantago lanceolata</i> L., buckhorn plan- tain.....	61	C	71	C	74	—	97	—
<b>Polygonaceae</b>								
<i>Rumex crispus</i> L., curly dock.....	34	C	37	C	48	C	93	C
<i>Rumex salicifolius</i> Wienn., willow dock..	60	—	31	—	85	C	68	C
<i>Rumex Acetosella</i> L., sheep sorrel.....	8	—	11	C	22	—	15	—
<i>Polygonum Persicaria</i> L., lady's thumb..	8	—	12	C	8	—	34	—
<i>Polygonum aviculare</i> L., knotweed.....	11	—	18	C	7	—	15	—
<b>Portulacaceae</b>								
<i>Portulaca oleracea</i> L., purslane.....	12	—	8	—	6	—	12	—
<b>Primulaceae</b>								
<i>Anagallis arvensis</i> L., red pimpernel....	81	—	81	C	81	C	31	—
<b>Ranunculaceae</b>								
<i>Ranunculus repens</i> L., creeping butter- cup.....	9	—	34	C	26	—	81	—
<b>Rosaceae</b>								
<i>Fragaria californica</i> C. & S., wood straw- berry.....	8	—	14	—	14	—	21	—
<b>Scrophulariaceae</b>								
<i>Linaria repens</i> Mill.....	8	—	8	—	5	—	4	—
<i>Scrophularia californica</i> Cham., figwort..	9	—	4	—	16	—	12	—
<i>Diplacus aurantiacus</i> (Curtis) Jepson, bush monkey-flower.....	15	—	12	—	7	—	7	—
<i>Veronica Buxbaumii</i> Tenore, Byzantine speedwell.....	26	C	23	C	15	—	34	—
<b>Solanaceae</b>								
<i>Datura Stramonium</i> L., Jimsonweed.....	10	C	11	C	7	C	14	C
<i>Solanum nigrum</i> L., black nightshade....	12	—	11	—	45	C	46	C
<b>Umbelliferae</b>								
<i>Conium maculatum</i> L., poison hemlock..	9	—	9	C	37	—	26	—
<i>Foeniculum vulgare</i> , fennel.....	10	—	49	—	47	C	35	C
<i>Oenanthe sarmentosa</i> Presl., water parsley	31	—	31	—	95	C	94	C
<b>Urticaceae</b>								
<i>Parietaria officinalis</i> L.....	5	—	12	—	20	—	25	—
<i>Urtica californica</i> Greene, coast nettle...	55	C	16	C	5	—	12	—
Total number of plant species in which life cycle was completed.....	..	19	..	25	..	27	..	28

\* Explanation of symbols: C = Life cycle completed; — = Life cycle not completed; x = no test made.

because occasionally the longevity of the leafhopper was greater than that of the plant, or a plant died prematurely. The same sources of error are applicable in these tests as in those for the life cycle, and a longer adult life might be obtained on any weed with additional trials.

## WEEDS EXPERIMENTALLY AND NATURALLY INFECTED

*Weeds Experimentally Infected.*—As shown in table 2, the virus was recovered from 25 species of weeds in 24 genera belonging to 14 families of plants after experimental infection by means of 1 to 4 vectors. One or more plants of six species of weeds indicated in this table showed characteristic aster-yellows symptoms after exposure to infective leafhoppers; but since the virus was not recovered from them, proof of infection is incomplete. Efforts were made to recover the virus from each of the 67 species of weeds inoculated, even if symptoms were not visible. In no case, however, was it recovered from a symptomless plant.

As may be seen by a comparison of tables 1 and 2, the plants showed no consistent connection in their host range to the virus and to the 4 vectors. Weeds susceptible to the virus were not always favorable food and breeding plants for the leafhoppers. Conversely, plants that proved to be favorable food and breeding plants were not always susceptible to infection.

The 4 vectors differed markedly in their ability to transmit the virus to healthy weeds. The number and percentages of weeds infected by each species of leafhopper, using 2 plants of each of the 25 susceptible species of weeds, were as follows: short-winged aster leafhopper 40, or 80 per cent; long-winged aster leafhopper 32, or 64 per cent; *Colladonus montanus* 16, or 32 per cent; and *Idiodonus geminatus* 12, or 24 per cent.

Table 2 shows the range and average period from inoculation by the vectors until the first symptoms developed in the weeds. There was a considerable range between the maximum, 68 days, and the minimum, 5 days. The incubation period of the disease in the plants was usually longer in winter than in summer, and was not the same for all species of weeds nor for all plants of a species.

*Weeds Naturally Infected.*—Forty-one species of weeds were demonstrated to be hosts of the virus under natural conditions and are listed below with their common names, their season's duration, and the locality in which they were collected.

## Amaranthaceae:

*Amaranthus retroflexus* L., rough pigweed; annual; Montara.

## Caryophyllaceae:

*Stellaria media* (L.) Cyr., common chickweed; annual; Milpitas.

*Spergula arvensis* L., corn spurry; annual; Montara.

## Compositae:

*Pieris echinoides* L., bristly ox-tongue; biennial; Montara.

*Lactuca scariola* L. var. *integrata* Gren. & Godr., prickly lettuce; annual; West Sacramento.

*Sonchus asper* L., prickly sow thistle; annual; San Jose.

*Sonchus oleraceus* L., common sow thistle; annual; Irvington.

*Erigeron canadensis* L., horseweed; annual or biennial; Irvington.

*Erigeron linifolius* Willd., flax-leaved fleabane; annual or biennial; Woodlake.

*Gnaphalium decurrens* Ives var. *californicum* Gray, California everlasting; biennial; Montara.

*Gnaphalium ramosissimum* Nutt., pink everlasting; biennial; Montara.

*Bidens frondosa* L., beggar-ticks; annual; Half Moon Bay.

TABLE 2  
WEEDS EXPERIMENTALLY INFECTED WITH VIRUS OF CALIFORNIA ASTER YELLOWS

Family and scientific name of plant	Season's duration	Number of plants showing symptoms of 2 inoculated by each of 4 vectors				Virus transferred to aster*	Incubation period of disease	
		Short-winged aster leaf-hopper	Long-winged aster leaf-hopper	<i>Colladonus montanus</i>	<i>Idiodonus geminatus</i>		Range days	Average days
Caryophyllaceae:								
<i>Stellaria media</i> L. (Cyr.)†	Annual	2	2	1	0	+	5-18	15
<i>Spergula arvensis</i> L.†	Annual	2	2	0	1	+	12-46	24
Compositae:								
<i>Lactuca scariola</i> L. var. <i>integrata</i>								
Gren. & Godr.†	Annual	2	0	0	0	+	19-20	20
<i>Aster chilensis</i> Nees	Perennial	0	1	1	0	-	11-22	18
<i>Gnaphalium decurrens</i> Ives var. <i>californicum</i> Gray†	Biennial	2	2	0	0	+	10-24	16
<i>Madia sativa</i> Molina	Annual	1	1	1	0	+	14-27	18
<i>Anthemis Cotula</i> L.†	Annual	2	1	1	2	+	5-24	13
<i>Matricaria suaveolens</i> (Pursh) Buch.†	Annual	2	1	2	0	+	8-33	20
<i>Cotula australis</i> Hook	Annual	2	2	2	0	+	18-22	20
<i>Centaurea melitensis</i> L.	Annual	1	1	0	0	+	13-23	18
<i>Centaurea Cyanus</i> L.	Annual	1	1	0	0	-	18-18	18
Cruciferae:								
<i>Brassica campestris</i> L.†	Annual	1	2	1	1	+	25-32	29
Dipsaceae:								
<i>Dipsacus fullonum</i> L.†	Biennial	2	1	0	0	+	15-29	22
Geraniaceae:								
<i>Geranium dissectum</i> L.	Annual	2	2	2	1	+	8-22	16
<i>Erodium moschatum</i> L'Her.†	Annual	2	2	1	2	+	14-20	17
Labiatae:								
<i>Lamium amplexicaule</i> L.†	Annual	1	1	0	0	+	26-33	30
Leguminosae:								
<i>Melilotus alba</i> Desr.	Annual	0	1	1	1	+	10-30	19
<i>Lotus salsuginosus</i> Greene	Annual	2	0	0	0	+	12-46	29
Malvaceae:								
<i>Malva nicaeensis</i> All.	Annual	2	2	2	1	+	12-21	18
Onagraceae:								
<i>Epilobium californicum</i> Hausskn.†	Annual	2	0	0	0	+	9-28	19
<i>Epilobium paniculatum</i> Nutt.†	Annual	2	0	0	1	+	23-36	28
Polygonaceae:								
<i>Polygonum aviculare</i> L.	Annual	0	1	0	0	+	39-39	39
Portulacaceae:								
<i>Portulaca oleracea</i> L.	Annual	1	2	1	1	+	23-53	36
Primulaceae:								
<i>Anagallis arvensis</i> L.†	Annual	2	2	1	0	+	15-68	26
Rosaceae:								
<i>Fragaria californica</i> C. & S.	Perennial	1	0	0	0	-	.....	..
Scrophulariaceae:								
<i>Scrophularia californica</i> Cham.	Perennial	2	2	2	1	-	.....	..
<i>Diplotis aurantiacus</i> Jepson	Perennial	1	0	0	0	+	11-11	11
<i>Veronica Buxbaumii</i> Tenore†	Annual	2	2	0	0	+	13-58	35
Solanaceae:								
<i>Datura Stramonium</i> L.	Annual	2	2	1	0	-	.....	..
<i>Solanum nigrum</i> L.†	Annual	2	2	0	1	+	12-22	16
Urticaceae:								
<i>Urtica californica</i> Greene	Annual	2	1	0	0	-	.....	..
Total		48	39	20	13	25		

\* The plus sign (+) indicates that the virus was transferred to aster, and the minus sign (-) shows that the virus was not recovered.

† Species of weeds demonstrated to be both naturally and experimentally infected with the virus.

## Compositae (Continued):

- Bidens pilosa* L., hairy bur marigold; annual; Half Moon Bay.  
*Hemizonia corymbosa* (DC.) T. & G., coast tarweed; annual; Half Moon Bay.  
*Helenium puberulum* DC., rosilla; perennial; San Jose.  
*Anthemis Cotula* L., mayweed; annual; Montara.  
*Matricaria suaveolens* (Pursh) Buch., pineapple weed; annual; Montara.  
*Senecio vulgaris* L., common groundsel; annual; Irvington.

## Cruciferae:

- Raphanus sativus* L., wild radish; annual or biennial; Centerville.  
*Brassica campestris* L., common yellow mustard; annual; Niles.  
*Roripa curvisiliqua* (Hook.) Greene, western yellow cress; annual; Geyserville.  
*Capsella Bursa-pastoris* (L.) Medic., shepherd's purse; annual; Irvington.

## Dipsacaceae:

- Dipsacus fullonum* L., fuller's teasel; biennial; Santa Clara.

## Geraniaceae:

- Erodium moschatum* L'Her., whitestem filaree; annual; Irvington.  
*Erodium cicutarium* L'Her., redstem filaree; annual; Montara.

## Labiatae:

- Lamium amplexicaule* L., dead nettle; annual; Salinas.

## Leguminosae:

- Medicago hispida* Gaertn., bur-clover; annual; Irvington.

## Malvaceae:

- Malva rotundifolia* L., dwarf mallow; annual; Berryessa.  
*Malva parviflora* L., cheese-weed; annual or biennial; Irvington.

## Onagraceae:

- Epilobium californicum* Hausskn., willow herb; perennial; Montara.  
*Epilobium paniculatum* Nutt., panicled willow herb; annual; Montara.

## Polygonaceae:

- Rumex Acetosella* L., sheep sorrel; perennial; Montara.  
*Polygonum Convolverulus* L., black bindweed; annual; Montara.

## Primulaceae:

- Anagallis arvensis* L., red pimpernel; annual; Alviso.

## Scrophulariaceae:

- Linaria canadensis* Dum., toad flax; annual; Woodlake.  
*Mimulus guttatus* DC., common monkey-flower; annual or biennial; Half Moon Bay.  
*Ilysanthes dubia* Barnh.; annual; Woodlake.  
*Veronica americana* Schwein., American speedwell; annual; Half Moon Bay.  
*Veronica Buxbaumii* Tenore, Byzantine speedwell; annual; Montara.

## Solanaeae:

- Solanum nigrum* L., black nightshade; annual; Montara.

As table 2 shows, 15 of the naturally infected species were included in the tests on experimental host range and were proved to be hosts under greenhouse conditions also.

Five weed species were found with typical symptoms of aster yellows, but the infection could not be demonstrated by recovery of the virus:

## Compositae:

- Xanthium canadense* Mill., cocklebur; annual; Woodlake.

## Geraniaceae:

- Erodium botrys* Bertol., broadleaf filaree; annual; Woodlake.

## Polygonaceae:

*Polygonum Persicaria* L., lady's thumb; annual; Woodlake.

## Solanaceae:

*Datura Stramonium* L., Jimsonweed; annual; Visalia.

## Umbelliferae:

*Ammi majus* L., bishop's weed; biennial; Napa.

The virus may overwinter in certain annuals that germinate during the autumn; in biennials and perennials; and in the vectors.

## SYMPTOMS ON INFECTED WEEDS

Several publications have described the symptoms of aster yellows on many plant species. The symptoms on aster have been described by Smith (1902); those on aster and other host plants by Kunkel (1927*a*, 1927*b*) and Severin (1929). No additional symptoms were observed on plants included in the weed-host range reported in this paper.

Symptoms produced on experimentally infected plants were not always identical in their degree of expression with those on weeds infected naturally in the field. There were several reasons: Plants grown under greenhouse conditions, especially when enclosed in cages, tend to become spindling and pale. Plants subjected to populations of insects often become weakened and stunted. Plants infected while young may fail to produce flowers, so that often the flower symptoms could not be ascertained. The effect of the disease on plant longevity was not uniform. Plants of some species died prematurely; the lives of others were apparently lengthened. Symptoms, though never entirely masked, were sometimes very mild. A few weed species partially recovered from severe symptom expression, such plants showing nearly normal shoots and flowers. Opportunity was not available to study the different stages of aster yellows on most naturally infected weeds, as was possible on experimentally infected plants. Symptoms on naturally infected weeds are therefore usually described from one stage only. In some instances, the infection was recent; in others, advanced. Several weeds had no flowers, so that floral symptoms could not be described for them.

The following is a brief description of the symptoms that appeared on experimentally and naturally infected weeds, from which the virus was recovered and transferred to healthy asters by previously noninfective short-winged or long-winged aster leafhoppers.

## AMARANTHACEAE, AMARANTH FAMILY

A single young naturally infected plant of rough pigweed (*Amaranthus retroflexus*) was collected, which showed vein clearing on several of the younger leaves.

## CARYOPHYLLACEAE, PINK FAMILY

Common chickweed (*Stellaria media*) both naturally and experimentally infected is extremely dwarfed, with stunted shoots rising from the leaf axils, often along the entire length of the stem. The stems are often twisted and curved, and the stunted tips of shoots are bent downward. The leaves are reduced in size, often rolled outward toward the petiole (plate 1, A), sometimes

forming a small ball. The shoot tips become rosetted through shortening of internodes and production of many stunted axillary shoots. The flowers are abnormal, with some or all parts of the perianth and gynoecium green, enlarged, and leaflike. Diseased plants sometimes live longer than healthy ones; and some severely infected show a tendency toward partial recovery, producing normal shoots and flowers from rosetted parts.

The early symptoms on experimentally infected corn spurry (*Spergula arvensis*) are elongation of the internodes of floral shoots, and chlorosis of leaves and stems; the stems become angled at the nodes and sometimes slightly twisted. Stunted, chlorotic axillary shoots are formed later, which, with the main shoots and leaves, tend to assume a vertical position. The flowers are abnormal and yellowish green, and often appear vegetative. The naturally infected plants examined displayed the following symptoms: They were stunted; all diseased parts were dwarfed; the stems and (less often) the leaves were chlorotic. The stems were spindling and showed curving and twisting. The flowers often were extremely dwarfed, almost vestigial. The sepals were enlarged, linear, and thick; their tips curved tightly inward over the remainder of the floral parts, which remained undersized; the number and size of their glandular hairs were strikingly reduced. The petals were green, especially over their basal two thirds, and smaller than normal. The stamens were dwarfed and usually lacked pollen. The gynoecium was reduced in size and often chlorotic.

#### COMPOSITAE, SUNFLOWER FAMILY

Affected parts of naturally infected bristly ox-tongue (*Picris echioides*) are spindling, chlorotic, with upright habit of growth, tending to become stunted, their parts reduced in size. The stems, especially the apical portions and young shoots, are often curved and twisted. The leaves commonly exhibit cleared venation; they are pale chlorotic green, narrowed, becoming linear and elongate, with reduction in size of the leaf spines. The upper apical leaves are often outwardly curled toward the petiole. The flowers are chlorotic and reduced in size, the involucre being much less affected than the remaining floral parts. In some plants the involucre may be only slightly reduced, its flowers chlorotic green; but when more severely affected, it may be extremely dwarfed, widely opened, almost scarious, with undeveloped flowers.

Cleared veinlets (plate 2, A) appear on the youngest leaves of both naturally and experimentally infected prickly lettuce (*Lactuca scariola* var. *integrata*), which become dwarfed. Stunted, chlorotic axillary shoots are produced, especially from the apical parts of the stem, bearing many chlorotic flower buds (plate 2, B). These buds generally become dry before expanding or, if they open, are yellowish green and wither quickly. The tips of such stems become rosetted because of shortened internodes with profuse production of axillary shoots.

The most conspicuous symptom on naturally infected common sow thistle (*Sonchus oleraceus*) is the bushy appearance of the infected plants, owing to the stunted, chlorotic axillary and apical shoots.

Prickly sow thistle (*Sonchus asper*) naturally infected with aster yellows shows numerous chlorotic shoots with curved petioles and upright outer

leaves (fig. 1). Infected tall plants are conspicuous in the field because of the stunted axillary shoots with dwarfed, yellow leaves.

The symptoms on naturally infected horseweed (*Erigeron canadensis*) are as follows: axillary shoots arising from the axils of the leaves on the main stem; stunted floral shoots bearing dwarfed, yellowish green flower heads, loosely expanded, with the corollas elongated.

Naturally infected flax-leaved fleabane (*Erigeron linifolius*) is stunted, with an enormous number of chlorotic axillary shoots bearing recurved linear leaves (fig. 2). The younger leaves on the main stem and often on the axillary shoots show cleared veinlets. The leaves are stiff and brittle. A purplish dis-



Fig. 1.—Naturally infected prickly sow thistle (*Sonchus asper*): longitudinal section of infected plant, showing chlorotic axillary shoots with curved petioles and upright outer leaves. (Santa Cruz, October 20, 1936.)

coloration occurs on the upper part of the main stem and axillary shoot, including the leaves.

The first symptom on experimentally infected California everlasting (*Gnaphalium decurrens* var. *californicum*) is a clearing of the veinlets on the younger leaves, often only on half the blade, the midrib then usually becoming curved. The plants soon appear dwarfed, the younger leaves being chlorotic, curled outward and downward. Stunted axillary shoots develop. The flowers are dwarfed, yellowish green, almost scarious, with loose involucres. The naturally infected plants observed did not show any marked stunting. Other symptoms were essentially those that appeared on experimentally infected plants.

Symptoms found on naturally infected pink everlasting (*Gnaphalium ramosissimum*) were rather obscure and were confined to the flower heads. The latter were but slightly chlorotic green; they were inconspicuously larger than normal heads, owing to a slight elongation of the florets and to a more

loosely expanded condition of the head instead of a compact arrangement as in the healthy head. The parts tend to be slightly more scarious than normal.

On beggar-ticks (*Bidens frondosa*) naturally infected with aster yellows, the younger apical leaves are dwarfed; and many of the older leaves are chlorotic, with vein clearing. The plants are dwarfed and develop stunted



Fig. 2.—Flax-leaved fleabane (*Erigeron linifolius*): left, main apical branch from a healthy plant; right, main apical branch from a naturally infected plant, showing an enormous number of axillary shoots bearing recurved, linear leaves. (King City, September 11, 1928.)

axillary shoots. The flower heads and the flowers themselves are usually very dwarfed and yellowish green. The bracts of the receptacle and flowers often are enlarged and spreading, so that the head is loosely open rather than compact.

Naturally infected *Bidens pilosa* exhibits symptoms essentially the same as those on beggar-ticks (*B. frondosa*). The proliferation of dwarfed, stunted

axillary shoots from nodes, especially on the apical parts of stems, is more profuse and striking than on the beggar-ticks.

Plants of naturally infected coast tarweed (*Hemizonia corymbosa*) are stunted; the internodes of the affected parts of the plants are greatly shortened. The most striking symptoms consist of abnormal flowers, from which are proliferated stunted, dwarfed, entirely vegetative, green, leafy shoots. The shoots occur mostly in loose clusters, resembling scattered green balls. In some less severe cases the floral parts are green, but in structure and arrangement are more recognizable as floral organs. Symptoms occasionally are confined to only one or a few branches of a plant.

On infected Chilean tarweed (*Madia sativa*), a transitory cleared venation appears on the younger leaves, which soon become chlorotic. With the onset of infection, plants quickly appear stunted. The youngest leaves are dwarfed, and all leaves tend to twist and to roll outward toward the petiole, sometimes to a marked degree. A young plant may resemble an umbrella because of severe stunting and the downward position of the leaves.

Naturally infected rosilla (*Helenium puberulum*) shows profuse axillary branching, with stunted, slightly chlorotic axillary shoots near the apex.

Mayweed (*Anthemis Cotula*) when experimentally infected with aster yellows becomes stunted at the tips of the shoots. Young leaves are chlorotic, dwarfed, curled outward and downward toward the petiole. Stunted, chlorotic axillary shoots are produced. The stems often are twisted and sometimes curved; and, during early stages of infection, the internodes usually become elongated. The combined effects of stunting, downward curling of the leaves, and production of axillary shoots cause a rosette condition at the tips of the shoots. The flowers are dwarfed, yellowish green, and usually abortive; their heads often fail to expand, and dry early. When flower heads do open, the ray flowers are greatly reduced, either white or yellowish green; and the disk flowers are somewhat enlarged and tend toward replacement of their parts by leaflike structures. On naturally infected plants the flower heads are usually reduced; the ray flowers are often normal white, sometimes suppressed and scarious. The receptacle is flattened in many flowers. The older leaves are commonly reddened.

On experimentally infected pineapple weed (*Matricaria suaveolens*) the symptoms produced by the virus are the same as those described for *Anthemis Cotula*. The tendency toward the rosette condition is somewhat more pronounced on most plants. No additional symptoms are expressed by naturally infected plants of this species.

On *Cotula australis*, experimental infection causes chlorosis and stunting of the tips of the stems. In early stages of the disease the internodes and petioles of young leaves sometimes become elongated. Later all growth is retarded, the internodes are greatly shortened, and the leaves are dwarfed, curling outward and downward toward the petiole. Chlorotic, stunted axillary shoots are produced, and the tips of the stems form rosettes. The flowers are much reduced in size, with pedicels shortened and all parts chlorotic. The longevity of some plants is increased. Partial recovery was observed in one: the chlorosis disappeared, new growth developed, and apparently normal flowers were produced.

The symptoms on naturally infected common groundsel (*Senecio vulgaris*) are as follows: spindling, chlorotic stems with the apical part crooked and often twisted; internodes somewhat lengthened; peduncles chlorotic, greatly elongated, and spindling; involucre reduced and loose; flowers yellowish green, with the gynoeceium and corolla elongated; disk flowers in extreme cases transformed into abnormal flower heads subtended by elongated spindling pedicels (plate 3, *A, B*). The pappus is sometimes absent.

Napa thistle (*Centaurea melitensis*) experimentally infected with aster yellows becomes stunted and spindling. The leaves are dwarfed and mildly chlorotic, assuming an upright position. Seven months after the first symptoms appeared, one plant developed flowers that were reduced in size but were apparently normal.

#### CRUCIFERAE, MUSTARD FAMILY

Wild radish (*Raphanus sativus*) naturally infected with aster yellows shows a clearing of the veins, and a slight chlorosis is evident on the younger leaves. A curvature of the midrib, a slight twisting of the petioles, and twisting and curvature of the stem occur. Flowers are green and often proliferated, with enlarged, thickened, green sepals; the petals reduced and colorless; the stamens enlarged, yellowish green, trilobed, leaflike; and the two carpels separate, dark green, and leafy.

Common yellow mustard (*Brassica campestris*), both naturally and experimentally infected with aster yellows, produces chlorotic axillary shoots and abnormal, green flowers on elongate, chlorotic peduncles. The pods on these peduncles are often greatly enlarged, curved, and flattened (plate 1, *C*) or sometimes become modified into 2 dwarfed floral shoots, which develop additional, abnormal flowers. The stems are often twisted and crooked. The floral shoots at first show accelerated growth; but later all floral and axillary shoots, flowers, and leaves become dwarfed. After periods of severe symptoms, occasional plants produce normal-appearing flowers.

Naturally infected western yellow cress (*Roripa curvisiliqua*) is stunted and dwarfed; leaves, especially the younger, are chlorotic; petioles are often curved or twisted; and pinnules show varying degrees of outward cupping. The older leaves tend to become flattened on the ground.

Shepherd's purse (*Capsella Bursa-pastoris*) naturally infected with aster yellows is stunted, with stems and peduncles of flowers thin and spindling. The flowers are often abnormal and dwarfed, with little chlorosis. They are usually normal in color, but develop dwarfed, compounded, floral shoots from the gynoeceium (plate 2, *C, D*).

#### DIPSACEAE, TEASEL FAMILY

The first symptoms of the disease on experimentally infected fuller's teasel (*Dipsacus fullonum*) was clearing of the veinlets and chlorosis of young leaves, sometimes only in localized areas on one side or near the base of a leaf. Growth occasionally was temporarily accelerated after the onset of the disease, the petioles of some leaves becoming slightly twisted. Later, plants were somewhat stunted, the leaves remaining faintly chlorotic and assuming an upright habit of growth. No flowers were produced. Individual flowers of

the affected floral heads of naturally infected plants are yellowish green and leaflike. The stem may continue growth through the terminal flower head, so that often more than one floral head is borne on a single stalk. The bracts are reduced and softened.

#### GERANIACEAE, GERANIUM FAMILY

Cut-leaved geranium (*Geranium dissectum*), experimentally infected with aster yellows, develops leaves with divisions reduced in number from 5 to 3, with entire margins. The younger and older leaves become cupped outward toward the petiole. In the first stages of the disease the petioles and primary shoots become elongated and chlorotic. Subsequent growth is retarded, spindling, and chlorotic; the internodes are shortened, and the leaves dwarfed (plate 1, *B*). Stunted axillary shoots appear, and the plants assume an upright habit of growth. The flowers are dwarfed and abnormal; the perianth and gynoecium often become leaflike and yellowish green. Plants are often rosetted through production of stunted axillary shoots from the crown.

Naturally and experimentally infected whitestem filaree (*Erodium moschatum*) develop dwarfed, chlorotic leaves with leaflets inwardly rolled along the margins. Stunted, chlorotic axillary shoots are produced from the crown or nodes of the stems. Often shoots continue to grow without reduction in length of the internodes, producing dwarfed axillary shoots that form rosettes at the nodes (plate 4, *A*). The tips of stems are chlorotic and often stunted. Abnormal flowers are formed, with all parts usually yellowish green, the sepals enlarged and crinkly (plate 4, *B, D*), the petals reduced and generally greenish but often normal in color, and the gynoecium shortened and enlarged. Often the replacement of the flower parts by vegetativelike structures is extreme, with the sepals and especially the carpels remarkably leaflike (plate 4, *C, D*). Affected leaves commonly become reddened during later stages of infection. Partial recovery is not uncommon among plants that have shown severe symptoms.

Symptoms of aster yellows on naturally infected redstem filaree (*Erodium cicutarium*) include general slight chlorosis of the entire plant, often with reddening of the outer, older leaves. The plants are stunted. Younger, inner leaves of crowns and shoot tips and apical leaves appear chlorotic and dwarfed. Petals and stems are often moderately twisted. Dwarfed, chlorotic axillary crowns are produced.

#### LABIATAE, MINT FAMILY

The apical part of the stem of experimentally infected dead nettle, or giraffe head (*Lamium amplexicaule*) becomes chlorotic and stunted, with mild chlorosis of the young leaves on the dwarfed plants. Stunted, chlorotic axillary shoots are produced. The flowers are abnormal and green, sometimes of usual size. Often, however, the calyx tube is elongated, and there is broadening of the tips of the sepals and petals, usually accompanied by an elongation of the pistil, which develops leaflike parts. Plants naturally infected are more severely stunted; and the gynoecia of abnormal flowers usually are transformed, each into a dwarfed shoot. The closely appressed, dwarfed, chlorotic, abnormal flowers form capitate heads at the tips of affected shoots.

## LEGUMINOSAE, PEA FAMILY

Bur-clover (*Medicago hispida*) infected in nature is stunted, showing twisted stems angled at nodes, with shortened internodes, stunted axillary shoots. Leaves are dwarfed, mildly chlorotic (fig. 3), with faint vein clearing.



Fig. 3.—Tip of a main branch of bur-clover (*Medicago hispida*) from a plant naturally infected with aster yellows, showing stunting, twisting, and angling of the stem at the nodes; shortened internodes; and stunted axillary shoots with dwarfed, mildly chlorotic leaves. (Irvington, January 11, 1939.)

Experimentally infected white sweetclover (*Melilotus alba*) develops numerous stunted axillary shoots on the dwarfed plants. The flower heads are dwarfed and chlorotic; the buds often become dry before expanding. Infected plants die prematurely.



Fig. 4.—Dwarf mallow (*Malva rotundifolia*) naturally infected with aster yellows, showing apical portion of shoot with cleared veinlets on the larger leaves and with dwarfed axillary shoots bearing outwardly rolled dwarfed leaves. A striking symptom is the enlarged green corolla. (Berryessa, September 26, 1934.)

*Lotus salsuginosus*, experimentally infected, is dwarfed. The stunted axillary shoots bear small, brittle, slightly chlorotic leaves, which later assume a reddish discoloration. The stems become angular at nodes. No flowers are produced.



Fig. 5.—Bull mallow (*Malva nicaeensis*) experimentally infected with aster yellows, showing outward-cupped older and younger leaves; and stunted axillary shoots forming a rosette at crown of plant.

#### MALVACEAE, MALLO FAMILY

Dwarf mallow (*Malva rotundifolia*) naturally infected with aster yellows shows cleared veinlets on the younger leaves, with yellow veinbanding on the older leaves. Small axillary shoots are developed that bear dwarfed, outwardly rolled leaves (fig. 4). A striking symptom is the enlarged green corolla (fig. 4). Plants infected when young present, in an advanced stage of the

disease, a dwarfed appearance, are bunched close to the surface of the ground, and have several large older leaves with greatly elongated petioles.

During early stages of experimental infection of bull mallow (*Malva nicaeensis*), the young leaves develop cleared veinlets and elongated petioles. Later the young leaves are dwarfed and display a unique condition in being upright in habit, stiff in texture, and slightly cupped inward toward the petiole. The blade is fluted, with the main veins lying in troughs, which are usually green adjacent to the veins, while the ridges between the troughs are chlorotic, with the chlorosis extending around the margin of the leaf. Sometimes older as well as younger leaves are cupped outwardly. Stunted, chlorotic axillary shoots are produced from the crown; these are upright in habit of growth. If infected while young, the plants become rosetted at the crown (fig. 5). Abnormal flowers are formed, with parts becoming leaflike and green.

The symptoms on naturally infected cheeseweed (*Malva parviflora*) are identical with those described for naturally infected *M. rotundifolia*.

#### ONAGRACEAE, EVENING PRIMROSE FAMILY

Willow herb (*Epilobium californicum*), both naturally and experimentally infected with aster yellows, becomes stunted and develops chlorotic axillary shoots. The young leaves are dwarfed and curled outward and downward toward the petiole. The midribs of many leaves are curved, forming asymmetrical halves of the blade on either side of the midrib. Green flowers are produced. Often the gynoeceum is transformed into a floral shoot that develops additional abnormal flowers.

Panicled willow herb (*Epilobium paniculatum*), both naturally and experimentally infected with the California aster-yellows virus shows the same symptoms as *E. californicum*; in addition, however, the elongate ovary often develops many very dwarfed shoots, which grow through the sides of the receptacle, the flower bud becoming abortive and dropping off without opening (fig. 6).

#### POLYGONACEAE, BUCKWHEAT FAMILY

Knotweed (*Polygonum aviculare*), experimentally infected, produced slightly chlorotic axillary shoots near the apical end of a main branch. These axillary shoots were somewhat stunted; their dwarfed leaves showed faintly cleared veinlets, which later took on a reddish coloration. Normal-appearing flowers and seeds were produced. The diseased plant outlived the controls by several months, continuing to make slow growth and to produce stunted axillary shoots. The symptoms were confined to one section of the plant only, and this was the last to die.

The only signs of aster yellows discernible on two plants of naturally infected black bindweed (*Polygonum Convolvulus*) were the abnormal, chlorotic, green proliferated flowers.

The most striking symptoms displayed by naturally infected sheep sorrel (*Rumex Acetosella*) were stunting and yellowing. The older leaves were generally tinged with red, the petioles often curved, and secondary crowns produced. Since no flowers were present on the plants observed, the floral symptoms could not be ascertained.

**PORTULACACEAE, PURSLANE FAMILY**

Experimentally infected common purslane (*Portulaca oleracea*) shows a spindling upright growth, with internodes somewhat elongated, and with the stems and leaves paler than normal. The apical leaves are dwarfed and chlorotic, and the younger leaves are usually bent downward from the base of the petioles. The stems are often twisted and slightly curved. The leaves drop early, and the plants die prematurely.



Fig. 6.—Panieled willow herb (*Epilobium paniculatum*): center, healthy flower from check or control plant, surrounded by four abnormal flowers from plant experimentally infected with aster yellows, showing stages in the development from the gynoecium of many dwarfed shoots, which grew through the sides of the receptacle. The abortive flower buds are still present on the two lower flowers.

**PRIMULACEAE, PRIMROSE FAMILY**

The growth of affected stems of experimentally infected red pimpernel (*Anagallis arvensis*) is accelerated during the early stages of infection. The stems are spindling, chlorotic, and often twisted, with elongated internodes. Young leaves near the tips of affected stems are cupped upward and slightly chlorotic. The flowers are subtended on elongated, spindling, chlorotic peduncles; the floral parts are yellowish green and sometimes greatly reduced.

Or, more often, the calyx is enlarged, the corolla is reduced, and the gynoecium develops into an abnormal shoot, with the carpels separated and leaflike. Naturally infected plants are dwarfed, with the stems twisted and slightly curved. The flowers are abnormal, with pedicels shortened; the calyx is enlarged and flatly expanded; the petals are reduced and are dark green, edged with magenta, or entirely magenta in color, cupped inwardly, or vestigial and yellowish. The gynoecium usually is reduced and flattened, sometimes on a peduncle; often the carpels are separated and leaflike.

#### SCROPHULARIACEAE, FIGWORT FAMILY

Toad flax (*Linaria canadensis*) naturally infected is dwarfed and chlorotic, with stunted axillary shoots arising from the basal section of the stems. Stems are often twisted. The flowers are abnormal and green, with floral parts replaced by leaflike structures.

The first symptom to appear on experimentally infected bush monkey-flower (*Diplacus aurantiacus*) consists of cleared veinlets and chlorosis of the youngest leaves. On some leaves these symptoms may be confined to the basal section on one side of the midrib. Later these midribs may become curved, causing asymmetrical leaves. The apical part of the stem becomes chlorotic. Chlorotic axillary shoots with short internodes develop, subtending reduced leaves with cleared veinlets and margins rolled outward toward the petiole. Apparently normal flowers are formed on symptomless branches of an infected plant, but no flowers are produced on the diseased branches.

Common monkey-flower (*Mimulus guttatus*) naturally infected with aster yellows is moderately dwarfed and spindling. The stems are chlorotic and often twisted. The leaves exhibit vein clearing and chlorosis. The flowers are reduced in size, and the floral parts are often chlorotic green.

Naturally infected crimson monkey-flower (*Mimulus cardinalis*) is dwarfed, with chlorotic stem tips. Stunted, chlorotic axillary shoots appear near the basal section of the plant.

*Ilysanthes dubia* naturally infected is dwarfed, with apical parts of the stems chlorotic. Stunted, chlorotic axillary shoots bear reduced, green flowers.

On American speedwell (*Veronica americana*) natural infection with aster yellows is manifested by chlorosis of the apical parts of shoots and leaves. Cleared venation is often visible on younger leaves. Affected shoots are somewhat spindling and tend to adopt an upright habit of growth. Stunted, chlorotic axillary shoots are sometimes produced at the nodes. The floral parts often are chlorotic green; and proliferated, chlorotic green, abnormal flowers are sometimes produced.

The leaves of naturally and experimentally infected Byzantine speedwell (*Veronica Buxbaumii*) develop faint, cleared veinlets; become reduced in size, broader, shorter, and more rounded; and are curled outward toward the petioles on the dwarfed plants. The apical parts of the stems are chlorotic and often twisted. Stunted, chlorotic axillary shoots are produced. The flowers are abnormal and yellowish green, and are subtended on elongated spindling peduncles that wither early. Some plants partially recover later. Similar symptoms are expressed on plants naturally infected, chlorosis and green flowers being the most striking of those exhibited.

### SOLANACEAE, NIGHTSHADE FAMILY

During early stages of both natural and experimental infection in black nightshade (*Solanum nigrum*), interveinal chlorosis often appears on the young leaves of the dwarfed plants, the main veins being banded with green. Cleared veinlets are present on some leaves. The leaves are sometimes cupped inward or outward; occasionally the margins are rolled inward toward the midrib. Often the midribs are curved, and the leaf margins indented. Many leaves are bent downward from the base of the petiole. New leaves are very dwarfed, chlorotic, and usually deformed. Stunted, chlorotic axillary shoots are produced from the buds in the axil of the leaves. In severe infections growth is greatly inhibited; the entire plant becomes yellowish green and rigid, and dies prematurely. No recovery takes place.

### HOST-RANGE DIFFERENCES BETWEEN CALIFORNIA AND NEW YORK ASTER YELLOWS

Kunkel (1926) was unable to infect plants belonging to the family Leguminosae with the virus of New York aster yellows. He states: "Yellows was not transmitted to any leguminous plant although many species and varieties were exposed under favorable conditions for infection."

Two species of weeds, white sweetclover (*Melilotus alba*) and *Lotus salsuginosus* in the family Leguminosae, proved susceptible to the virus of California aster yellows under greenhouse conditions (table 1); and one species in the same family, bur clover (*Medicago hispida*), was proved to be infected under natural conditions. It is not known whether any of these three species in the Leguminosae were included among those species tested by Kunkel. Conceivably, however, the susceptibility of these Leguminosae may constitute another difference between the strains of California and New York aster yellows.

Overlapping host ranges of the viruses of California and New York aster yellows include the following 3 species of weeds: *Plantago major* (Severin, 1929), *Erigeron canadensis*, and *Sonchus oleraceus*, belonging to two families.

### SUMMARY

Leafhopper vectors of California aster yellows completed their life cycles on various weed species as follows: short-winged aster leafhopper (*Macrostelus divinus*), 19 species; long-winged aster leafhopper (*M. divinus*), 25 species; mountain leafhopper (*Colladonus montanus*), 27 species; and geminate leafhopper (*Idiodonus geminatus*), 28 species.

The longevity of adult males of the 4 vectors on 67 weed species was compared.

Experimentally, 25 species of weeds in 24 genera belonging to 14 families were infected with the aster-yellows virus by means of 1 to 4 vectors, including 22 annuals, 2 biennials, and 1 perennial. The virus, recovered by previously noninfective short-winged or long-winged aster leafhoppers from the infected weeds, was transferred to asters. Six species of inoculated weeds developed symptoms of aster yellows, but the virus was not recovered from them. Partial disappearance of symptoms occurred in some of the species.

In all, 41 species of weeds in 31 genera belonging to 14 families were demonstrated to be naturally infected with the aster-yellows virus, including 28 annuals, 5 annuals or biennials, 4 biennials, and 4 perennials. The virus was recovered by previously noninfective short-winged or long-winged aster leafhoppers from the infected weeds and transferred to asters. Although 5 additional weed species showed typical symptoms of aster yellows under natural conditions, all efforts to recover the virus from them were unsuccessful. The virus overwinters in annual, biennial, and perennial weeds and in its leafhopper vectors.

Host-range differences included 3 species of weeds, in the family Leguminosae, apparently reacting differently to the California and New York strains of the aster-yellows virus, although it is not known whether these species were subjected to experimental infection by Kunkel. Overlapping host ranges of the two strains of viruses include 3 weed species.

The symptoms are described for each weed species proved to be either experimentally or naturally infected with the virus.

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## PLATES





Plate 1.—A, Common chickweed (*Stellaria media*) experimentally infected with aster yellows, showing outward rolling of the leaves toward the petioles. B, Cut-leaved geranium (*Geranium dissectum*): upper left, apical end of stem from healthy check or control plant; upper right, tip of stem from an experimentally infected plant, showing retarded, chlorotic, and spindling growth with dwarfed leaves; lower left, gynoeceum from normal plant; lower center, dwarfed floral shoot with small, abnormal, yellowish-green flowers; lower right, leaf from an experimentally infected plant, showing outward cupping toward the petiole. C, Common yellow mustard (*Brassica campestris*): left, tip of floral shoot from healthy plant used as a check or control, showing normal flowers and pods; upper center and right, tips of floral shoots from plants experimentally infected with aster yellows, showing abnormal green flowers on elongated, chlorotic peduncles; lower center, diseased flowers with enlarged, curved, and flattened pods.



Plate 2.—A, B, Prickly lettuce (*Lactuca scariola* var. *integrata*): A, Left, leaf from healthy plant; right, three leaves showing cleared venation. B, Apical part of main branch, showing axillary shoots and numerous yellowish-green flower buds. (West Sacramento, October 9, 1931.) C, D, Shepherd's purse (*Capsella Bursa-pastoris*) naturally infected with aster yellows. C, Center, tip of floral shoot from healthy plant; left and right, apical end of floral shoots from diseased plants naturally infected with aster yellows, showing thin, spindling stems and peduncles; abnormal, dwarfed flowers; and dwarfed, compounded floral shoots developing from the gynoeceium. D, Compound floral shoot originating from the gynoeceium of a single abnormal flower. (Irvington, January 13, 1939.)



Plate 3.—Common groundsel (*Senecio vulgaris*): A, Center, flower head from a healthy plant, surrounded by four abnormal flower heads from plants naturally infected with aster yellows, showing chlorotic, elongated, and spindling peduncles; reduced, loose involucre; and yellowish-green disk flowers subtended by elongated, spindling pedicels. B, Single abnormal flower head from a plant infected with aster yellows under natural conditions, showing abnormal, chlorotic disk flowers subtended on elongated, spindling pedicels. (A and B were collected at Irvington, January 13, 1939.)



Plate 4.—Whitestem filaree (*Erodium moschatum*), from plants naturally infected with aster yellows: A, part of stem showing rosette formation at node by dwarfed axillary shoots; B, floral cluster at apical end of shoot, showing stunting, chlorosis, and several stages of phyllody; C, D, single abnormal flowers greatly enlarged, showing two stages of phyllody.





